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Phylogenetic and Ecological Significance of Variation in the Scleral Ring of Aquatic Foraging Birds

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Phylogenetic and Ecological Significance of Variation in the Scleral Ring in Aquatic Foraging Birds

by

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Abstract

Phylogenetic and Ecological Significance of Variation in the Scleral Ring of Aquatic Foraging Birds

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Diving birds must accommodate their vision to air and water, two very different optical media. A few species, such as penguins (Sphenisciformes), dive to depths approaching the aphotic zone of the ocean and must accommodate their vision to both the change in media and significant light attenuation. Previous studies show that optical properties of the eye e.g., pupil aperture and focal length, are reflected in the eye's gross morphology and have a strong positive correlation with osteological proxies from the orbit and scleral ring. This study combines qualitative and quantitative measurements utilized in previous studies to create a larger feature space for classification. A total of 170 species were evaluated for distinct classes of eye shape, 87 of which were newly measured species of Charadriiformes, Procellariiformes, "Pelecaniformes", and Sphenisciformes. Unlike in previous studies of land birds, no pattern was recovered in eye shape based on the light levels where the birds foraged. Aquatic birds are active in a wide range of conditions; foraging both day and night and at varying water depths based on the time of year and available prey. Diverse aquatic bird ecology probably contributes

to the lack of distinct eye shape classes based on dive depth. Regression analysis was able to recover prey capture style (i.e., plunge, pursuit, skimming, or wading) based on orbit and scleral ring measurements. Misclassification was most common in taxa that exhibited multiple modes of prey capture such as the albatross (Diomedeidae). The ability to determine foraging style based on osteological eye measurements may have implications for identifying prey capture method in extinct species of aquatic birds.

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Chapter 1: Quantitative Analysis of the Relationship between Scleral Ring Morphology and Aquatic bird Foraging

Aquatic birds must navigate two optically different media, air and water. A few species, such as penguins (Sphenisciformes), dive to depths approaching the aphotic zone of the ocean and must accommodate their vision to both the change in media and significant light attenuation. Optical properties of the eye (e.g., pupil aperture and focal length) are reflected in the gross morphology of the eye and have been shown to have a strong positive correlation with osteological proxies from the orbit and scleral ring. While a relationship between scleral ring morphology and activity pattern in living birds has been recovered, aquatic avian taxa have not been evaluated. Aquatic birds are active in a diverse range of light conditions and optical media. Many diurnal birds dive into the early evening during breeding season. Here we address how aquatic birds compare to non-aquatic birds with respect to a relationship between morphology and activity pattern. In addition, we look at how unique features of aquatic foraging such as dive depth and prey capture method affect the shape of the eye. This study combines measurements of osteological features of the eye utilized in previous studies with a measurement of scleral ring height to create a larger feature space for classification of ecology based on scleral ring morphology. A total of 170 species were evaluated., 97 of these species were newly measured taxa of from Charadriiformes, and the waterbird clade including Procellariiformes, Ciconiiformes, "Pelecaniformes" and Sphenisciformes. Logistic regression and neural networks were used to evaluate activity pattern. Logistic regression based on orbit and scleral ring measurements recovers clusters described by different

styles of prey capture (i.e., plunge, pursuit, skimming, or wading). Misclassification of dive type is most common in birds that exhibit multiple modes of prey capture. Many diving birds hunt at varying depths depending on the location of the prey species in the water column. The diversity of ecological conditions under which pelagic seabirds live probably contributes to the lack resolution in analyses of dive depth and diurnal/nocturnal activity. However, prey capture method is consistent amongst individuals and influences the morphology of the eye.

INTRODUCTION

There is a strong correlation between gross eyeball morphology and activity pattern in birds (Hall and Ross 2007, Hall 2008, Schmitz 2009). In birds, where a large portion of the head is dedicated to the visual system there is a strong link between activity pattern and eye shape (Hall and Ross 2007, Hall 2008). Bird eyes fit tightly into the orbit with little fatty padding and reduced ribbon-like oculorotary muscles laying snuggly against the globe of the eye (Walls 1942). As a result of the reduced musculature, the size of the orbit is a good approximation of the size of the soft tissue of the eye.

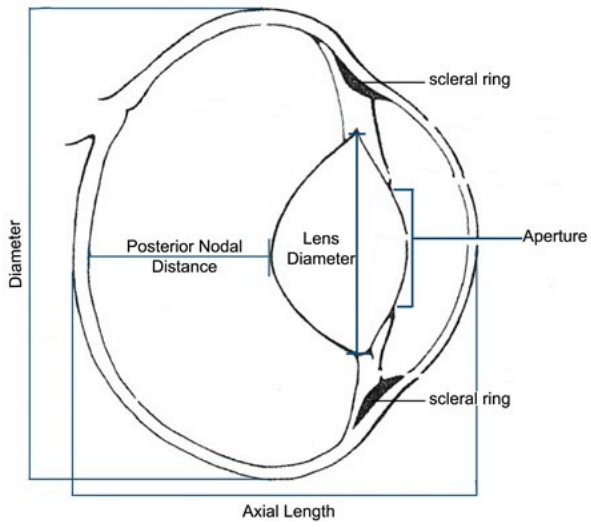

Figure 1. Cross section of the eye and scleral ring

A cross-section through the eye and scleral ring modified from Sivak (1980) shows the optical features of the eye: aperture, diameter, and posterior nodal distance. These features vary to increase or decrease sensitivity making the eye more or less optimized for nocturnal activity. These optical features correlate well with measurements of the scleral ring and orbit.

Previous studies by Hall and Ross (2007) and Schmitz (2009) have both corroborated the excellent correlation between osteological measurements of the orbit and scleral ring to gross morphology of the eye (Figure 1). Orbit length gives an approximation of total eyeball diameter with a coefficient of correlation value of 0.95 (Schmitz 2009). Orbit length corresponds to eyeball diameter, with an r^2 value of 0.95 (Schmitz 2009), internal scleral ring diameter corresponds to corneal size, r^2= .98 (Hall and Ross 2007), and scleral ring height corresponds to axial eye length, r^2 = .87 (Hall and Ross 2007). Prior studies did not include many aquatic birds and left out the deepest

diving species of Charadriiformes, murres and guilletmots, as well as the puffins and most penguins. This study evaluates how aquatic bird eye morphology compares to non-aquatic bird eye morphology based on activity pattern. Within aquatic taxa, the effects of dive depth and prey capture method are also evaluated as potential influences on the gross morphology of the eye as ocean light levels vary from full sun to minimal star light illumination based on depth in the water column (Jerlov 1969, Martin 1999).

Some aquatic birds dive to depths were the light is attenuated to levels similar to terrestrial nighttime illumination. Penguins are considered the most aquatic of birds and spend most of their life in the ocean with exceptions of when they come on land to breed (Walls 1942, Kooyman 1975). The largest penguins, *Aptenodytes forsteri* and *Aptenodytes patagonicus*, can dive well below 200 meters where ocean light levels are attenuated to level approaching a minimum star lit night on land (Figure 2)(Martin 1999). It has been suggested that penguins hunt for Lantern fish in the dim light of the deep ocean by identifying the point bioluminescence of their prey (Martin 1985). Identifying weak point light sources deep in the ocean would require a very sensitive eye. We may expect penguin eyes to have a morphology optimized for greater sensitivity and less acuity to allow hunting at low light levels.

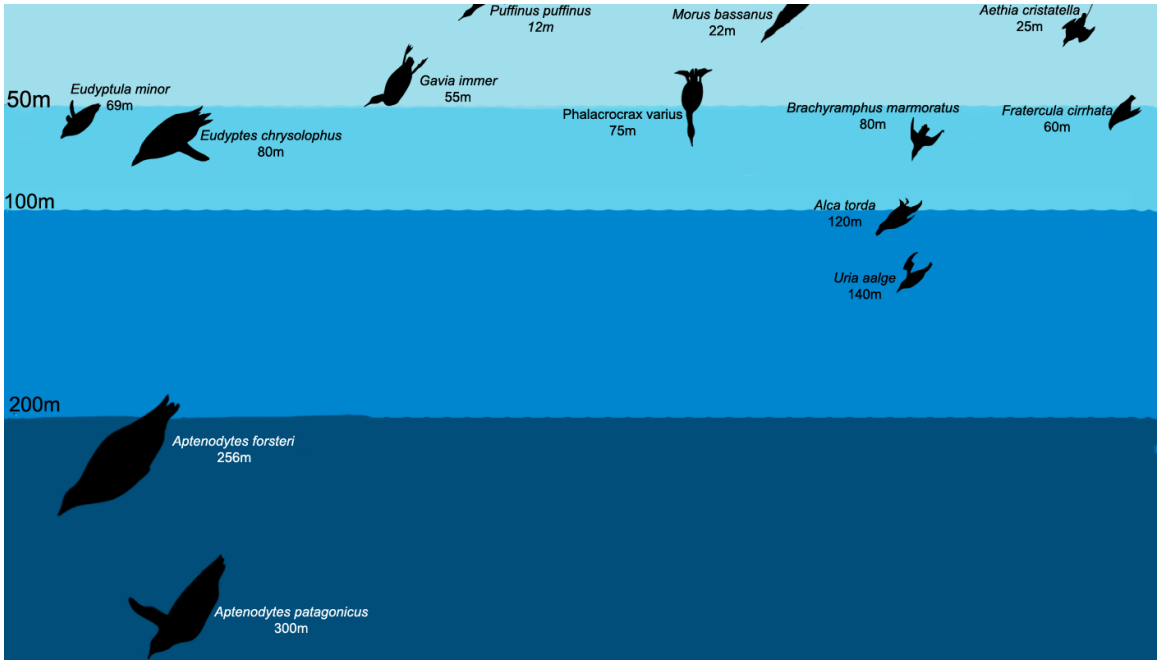

Figure 2. Dive depth and illuminance

Maximum dive depths for a selection of species from waterbirds (clade H) and Charadriiformes. Ocean illuminance is indicated by color with the lightest layers representing the euphotic zone (terrestrial daylight conditions) and the decrease to the darkest layer equivalent to light levels on a moonlit night.

In order to quantify the relationship between the nocturnal/diurnal activity pattern and the osteological eyeball correlates of internal scleral ring diameter (INT), external scleral ring diameter (EXT), and orbit length (OL) in non-aquatic avian species and aquatic species, a regression analysis was performed. Activity pattern classification and skeletal measurements on non-aquatic taxa were taken from the Schmitz (2010) study. Activity pattern for aquatic taxa was taken from various studies on foraging in aquatic bird (Appendix B). Most studies of aquatic birds occur while they nest on land during breeding season. As a result, most data is divided between time spent foraging and time

spent in nest attendance and breeding activity. For this study, We consider the time of day when the bird was foraging as its active period; therefore birds that forage at night and attend their nest during the day are classified as nocturnal. Schmitz (2010) discovered a fairly linear relationship between osteological features and nocturnal and diurnal activity pattern. I hypothesize that the varying light conditions in the ocean will cause the aquatic birds to differ from terrestrial birds in their classification of activity pattern as a result of light attenuation in the ocean. A more nocturnal eye shape would be predicted in the deepest diving taxa such as *Aptenodytes patagonicus* and *Aptenodytes forsteri*. This study will also investigate if there is an influence on the morphology of the scleral ring as a result of variation in dive depth and prey capture method.

MATERIALS AND METHODS

Study Animals

Data were collected on 317 specimens from 87 non-passerine bird species (Appendix A). Study groups include: 38 species of Charadriiformes (22 auks, 1 skua, 5 gulls, 5 terns, 1 skimmer, 2 sandpipers, and 2 killdeer), 14 species of Procellariiformes (4 albatrosses, 3 shearwaters, 1 fulmar, 1 storm petrel, 2 diving petrels and 3 gadfly petrels), 10 species of Spheniscidae (penguins), 3 species of Gaviidae (divers), 1 species of Podicipedidae (grebe), 13 species from core "Pelecaniformes"(3 gannets, 6 cormorants, 2 darters, and 2 frigate birds), 8 species from a monophyletic Ciconiiformes including 3 pelicans as well as 3 herons, 1 ibis, and 1 hamerkop. Specimens were obtained from The

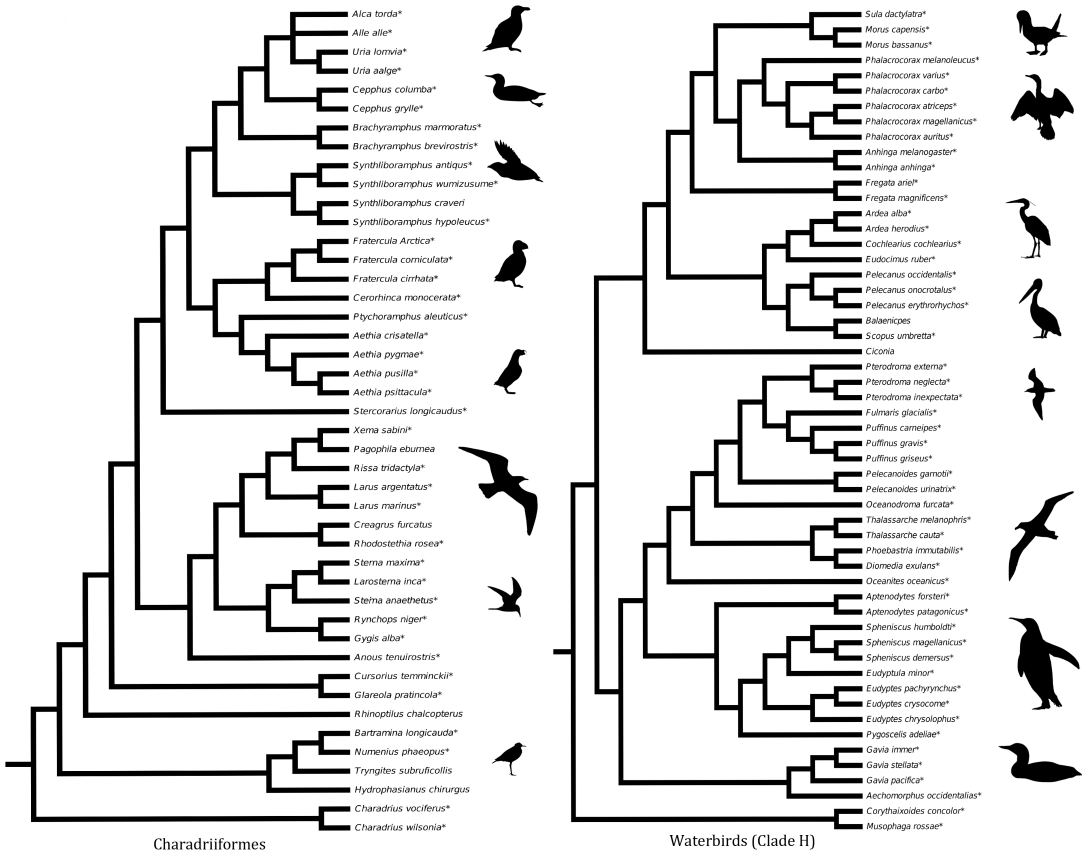

Figure 3. Phylogenies of the waterbird and Charadriiform clades

Waterbird clade based on Hackett et al. (2008) and Charadriiformes based on Smith (2011). The asterisks indicate species that were measured for this study.

American Museum of Natural History (New York), United States Museum of Natural History (Washington D.C), Burke Museum (Seattle), Vertebrate Paleontology Lab at The University of Texas at Austin. Measurements for non-aquatic birds were taken from the study by Schmitz (2010), this data set includes 77 avian species.

All specimens are from the water bird clade (Clade H of Hackett et al. 2008) and Charadriiformes (Figure 3). For the latter taxon, the phylogeny of Smith et al. (2011) was used. The focus of this study is on birds that utilize underwater pursuit diving to capture

prey. During measurement collection, every effort was made to measure equal numbers of male and female representatives from each species; however availability of skeletons, varying quality of preservation, and time constraints made this impossible. Species are represented by an average of 5-10 individuals with at least two individuals measured unless otherwise noted.

Measurements

Osteological measurements correlated with eyeball morphology were taken using digital calipers to the nearest 0.01mm (Appendix A). Measurements from the skull include orbit length (OL), measured from the most anterior to most posterior point of the orbital margin (Von Den Driesch 1976) (Figure 4).

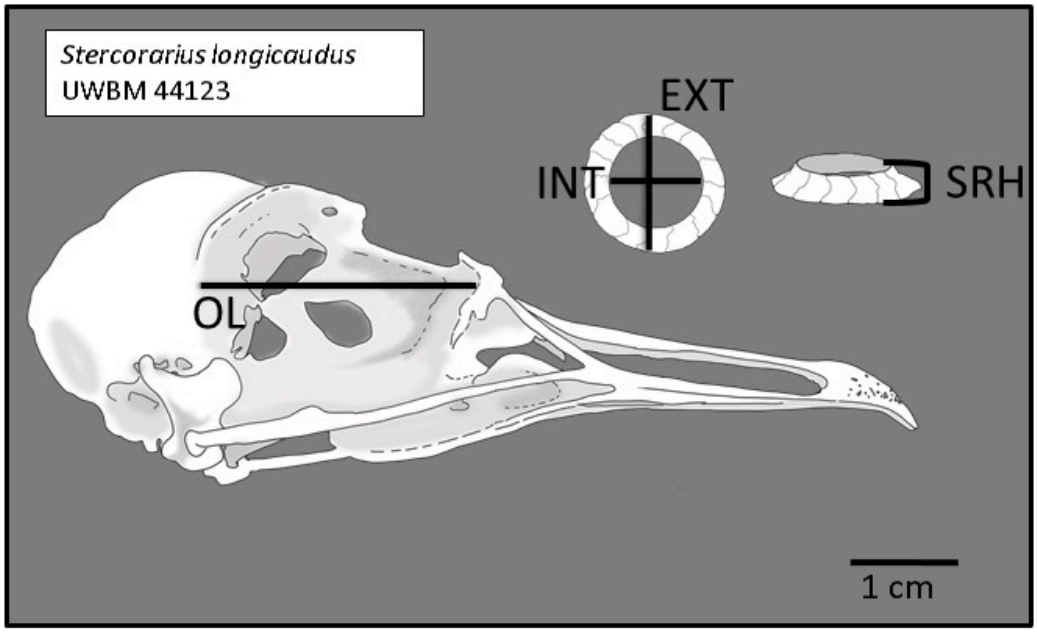

Figure 4. Measurements of the orbit and scleral ring

Diagram of the measurements taken from the skull and scleral ring of each specimen. OL, orbit length; INT, internal scleral ring diameter; EXT, external scleral ring diameter; SRH, scleral ring height

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Measurements were taken from scleral rings associated with the skulls as long as they were not broken, severely warped, or completely obscured by dried scleral tissue. In specimens where one scleral ring or orbit was damaged, only the intact scleral ring or orbit was measured. The left and right values were averaged for use in this study. Measurements of the scleral ring include: internal scleral ring diameter (INT), external scleral ring diameter (EXT), and scleral ring height (SRH) (Figure 3). Schmitz (2010) found that a ratio of only INT and EXT showed a strong bias towards body size with smaller species erroneously classified as diurnal and larger species as nocturnal. To avoid this, Schmitz (2010) added a new character, OL, to increase the number of dimensions available for analysis. Here we include, SRH as a fourth morphological character to increase the dimension space further and aid in classification.

Methods

A bivariate plot comparing aquatic and non-aquatic birds shows a distinction between nocturnal birds and diurnal and cathemeral birds. The data set consisted of 34 aquatic birds and 70 non-aquatic birds. The number of aquatic taxa was limited by the data available on the time of day when each species was foraging in the literature (Appendix B). A Polynomial regression analysis was performed using a second-degree quadratic kernel of EXT, INT and OL to identify nocturnal birds from the terrestrial bird

data set. The regression analysis performed 100,000 iterations to solve the weighted least squares problem and generate a more robust test. A skewed weighting factor of 0.3 in favor of nocturnality was used as a cut-off, since the data set was bias in favor of diurnal birds. The resulting scatter plot was visualized in MATLAB with the aquatic bird measurements plotted with non-aquatic birds (Figure 5). Variation-bias error calculations were performed to test for over-fitting of the data.

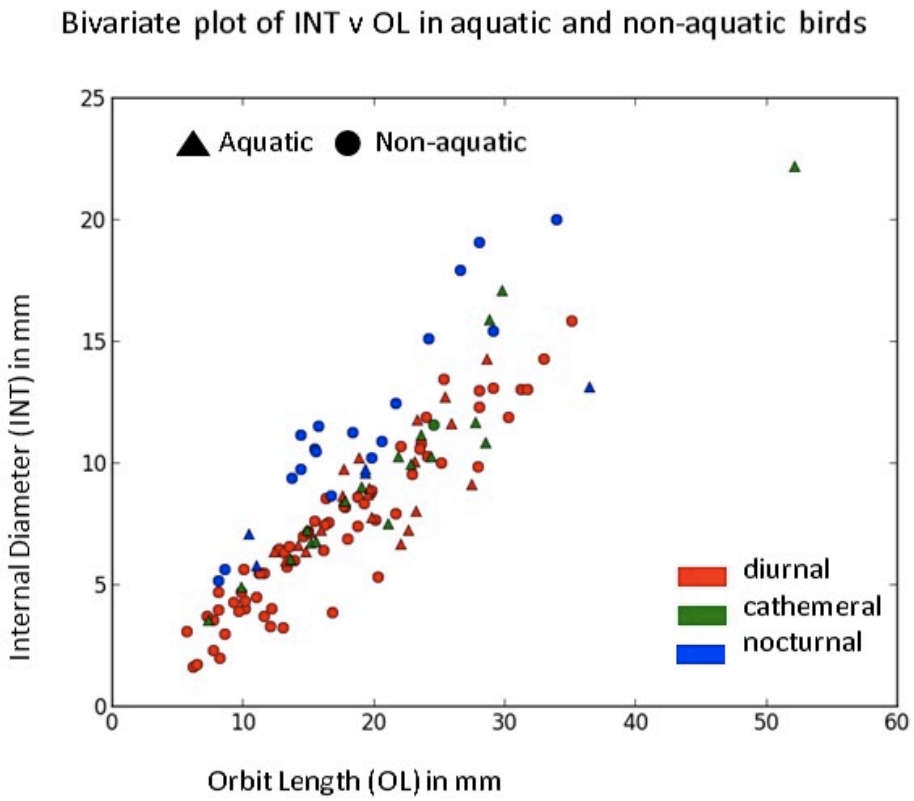


Figure 5. Bivariate plot of INT v OL

Plot of INT and OL in aquatic birds (triangles) and non-aquatic birds (circles) based on activity pattern. A linear separation between the diurnal (red) and nocturnal (blue) species with cathemeral (green) species overlapping both.

In order to test the hypothesis that deep diving aquatic birds are adapted to lower light levels resulting in more nocturnal eye shape, a neural network was used to look at the relationship between dive depths and measurements of OL, INT, EXT and SRH (Figure 6). The amount of light available at different depths in the ocean varies based on the turbidity, salinity, and temperature of the water (Jerlov 1969). To approximate the illuminance of the ocean, Jerlov's classification for type 1 oceanic waters was used (Jerlov 1969). The maximum dive depths were obtained from the literature (Appendix C). Many surface feeding species have not been evaluated for maximum diving depth and could not be used in the dive depth analysis. A standard artificial neural network was created using feed-forward connections between neurons that uses back propagation for training (Kramer 1991).

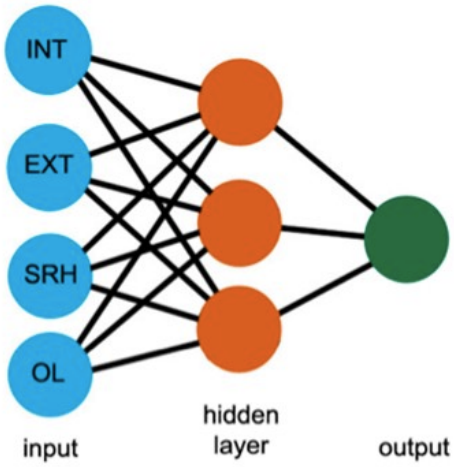


Figure 6. Neural Network

The neural network consists of 4 input layers (blue) of INT, EXT, SRH, and OL connecting to each of the hidden layers (orange) that compress the data and connect to

the output layer (green). The output layer was changed to generate continuous values for dive depth and discreet values for dive style.

The advantage of neural networks is their ability to find non-linear patterns in data sets. Since the relationship between the four measurements of OL, INT, EXT, and SRH had not been evaluated before a neural network allows the exploration of many potential patterns. However the non-deterministic nature of neural networks results in the need for multiple runs to establish an optimal solution. A second potential problem is the ability of the neural network to over fit the data and find a pattern where none exists. To detect over fitting the results need to be cross-validated after the test is run. To determine that the network has found the optimal solution it was run 10,000 times and the consensus result was taken. The construction of this network consisted of four inputs, one for each osteological measurement (OL, EXT, INT, SRH) and a single continuous output variable for dive depth. The hidden layers within the neural network contained three neurons in a single layer that compresses the data and concentrates the information before reconstructing the data in the out layer (Sanger 1989). A small single layer network was used to avoid over-fitting the data, which previous analysis showed usually exhibits a linear to quadratic relationship (Schmitz 2010).

Training sets were generated using 80% of the data, specimens were randomly selected by the computer from the diving dataset (Appendix C). The networked trained for 1,000,000 iterations to establish that stable weights had been obtained between the neurons. 10% of the data, which was not used for training, was used as a test set. The remaining 10% of the data was used as a cross-validation set as a second test against

over-fitting in the model. The standard error for both the training and test sets were calculated to create a variation-bias statistic that measures over-fitting in the network (Sanger 1989).

A second analysis was performed on the style of prey capture each species uses most frequently; five styles were identified: pursuit diving, plunge diving, surface diving, surface seizing, and dipping. A second single layer neural network was set up using the same parameters as the network used to test dive depth. The output neuron was changed to a discrete value that corresponded to each of the dive styles. The networked trained on 80% of the data for 1,000,000 iterations before testing on 10% of the data and running cross-validation on the final 10% of the data.

Based on results from the neural network, a polynomial regression analysis was performed to classify dive style. A cubic kernel of INT, EXT, SRH, and OL were used to try and identify the pursuit diving style using logistic regression. A basic gradient descent optimization algorithm was used. The resulting score is an output of logistic regression without a cut-off. Classification is possible once a cut-off is established, the default value is 0.5, but skewed class ratios will alter where this cut off should be drawn on the score column. As only one dive style can be tested at a time, the cut-off was established in favor of the selected dive style, pursuit diving.

A supertree was constructed that takes the Hackett et al. (2008) topology as its base. As the relationships among all species sampled here were not investigated in that analysis, placement of these taxa was based on phylogenies from the following studies: McCracken and Sheldon 1998, Nunn and Stanley 1998, Kennedy et al 2000, Hackett et al

2008, Kspeka and Clarke 2010. A separate tree was constructed for Charadriiformes based on the phylogeny from the study by Smith (2011). Phylogenetic relationships for each of the morphological characters were evaluated using Pagel's lambda (Pagel 1999). Pagel's lambda evaluates the extent to which traits are correlated based on a shared evolutionary history, no phylogenetic correlation has a value of 0 and high correlation has a value close to 1.

RESULTS

The logistic regression analysis, including non-aquatic birds from Schmitz (2010), was able to classify the nocturnal and diurnal terrestrial birds with 96% accuracy. Supporting the ability to distinguish non-aquatic nocturnal and diurnal birds. All birds were correctly classified with the exception of one nocturnal species (*Tyto alba*) and two diurnal species (*Melagris gallopavo* and *Strix occidetalis*). The accuracy for the regression analysis is slightly higher than those in Schmitz (2010) as the results were not weighted by the phylogeny.

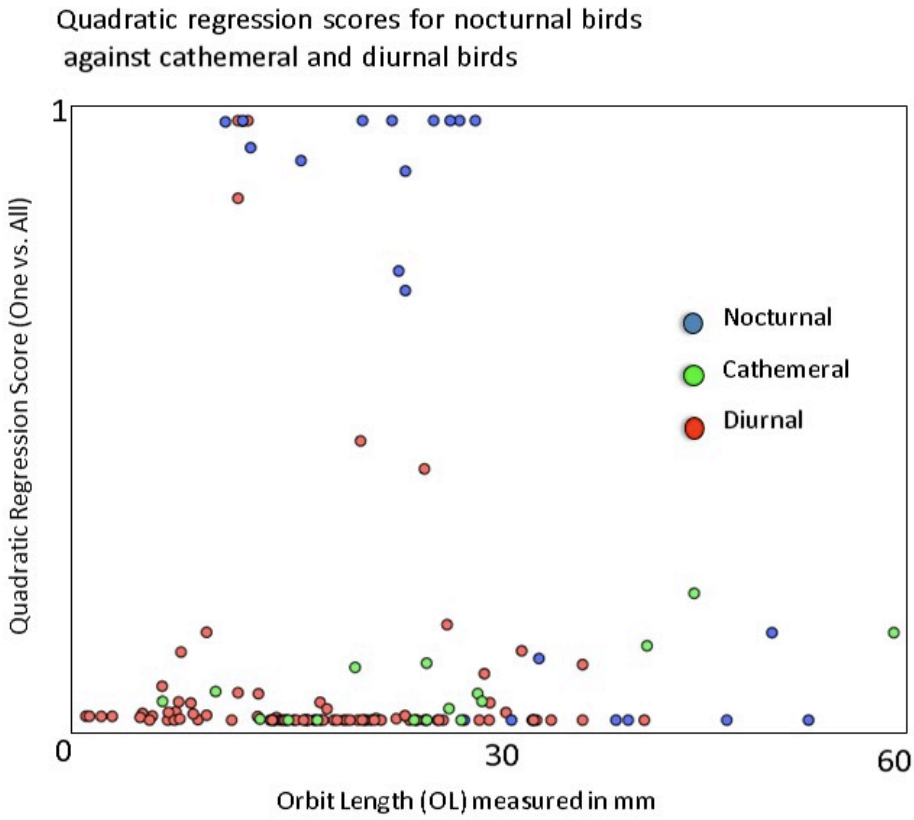


Figure 7. Quadratic regression of nocturnal birds v other

Quadratic regression of INT, EXT and OL for aquatic and non-aquatic birds with values close to 1 being certain the individual is nocturnal and values of 0 being certainly not nocturnal. Most nocturnal birds (blue) are correctly classified near the top and diurnal birds (red) and cathemeral birds (green) are correctly placed near 0.

A second regression analysis was performed using OL, INT and EXT for a combination of aquatic and non-aquatic bird data and included nocturnal, diurnal, and cathemeral birds (Figure 7). SRH was not included in the analysis since it was not measured for the birds in the Schmitz (2010) dataset. The regression classified 70% of the birds accurately with most of the error resulting from an inability to distinguish

cathemeral from diurnal birds. These results are similar to the findings of both Schmitz (2009) and Hall (2008). Cathemeral birds cannot be distinguished from diurnal birds using the INT and EXT scleral ring and orbit measurements alone. Phylogenetic relationships for each of the morphological characters were evaluated using Pagel's lambda (Pagel 1999).. All measurements were calculated separately and had Pagel's lambda values close to zero indicating phylogeny was not a strong influence. As a result, all analyses were run without weighting for phylogenetic signal.

The neural network utilizing INT, EXT, OL, and SRH with a single continuous output of dive depth was unable to predict dive depths within an average of 30 meters of the numbers recorded in the literature for species. The training set consisted of 51 aquatic birds with 13 birds reserved for tests and cross-validation. The network had an average deviation of predicted dive depth between 5 and 30 meters. The square error for the test set was 0.42 indicative of the poor predictive power of the function described by the network.

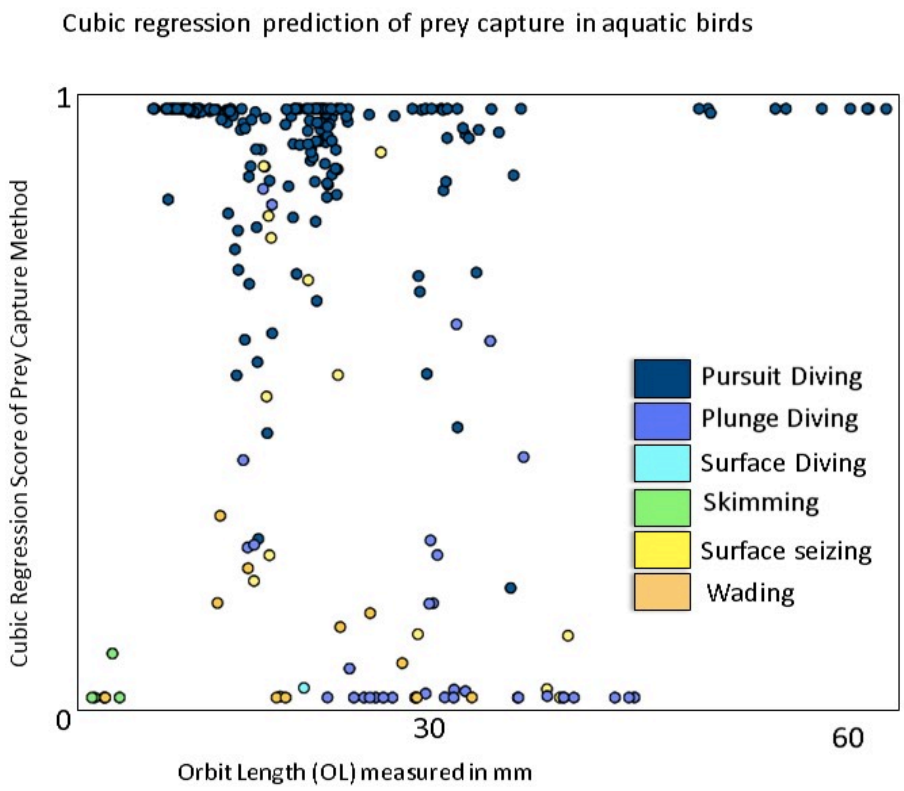


Figure 8. Cubic regression on dive style

Cubic regression of aquatic bird species as individuals showing regression scores for pursuit diving (dark blue) versus all other dive styles. The species with scores close to 1 are classified as pursuit and those species with values close to 0 are classified as non-pursuit divers.

The dive style neural network utilizing INT, EXT, OL, and SRH with a single discreet out put was able to predict the dive style of the test set. The training set consisted of 56 aquatic birds with 14 birds excluded for use in the training and cross validation sets. The function that best described the relationship between the osteological measurements of INT, EXT, SRH, and OL and the dive style was a cubic function (Figure 8). Cubic regression was performed to separate pursuit divers from the other dive styles. Bias-

variation numbers were low and did not indicate over-fitting with a cubic polynomial. All penguins (Sphenisciformes) and auks (Alcidae) were correctly recovered as pursuit divers with the exception of the Adelie penguin (*Pygoscelis adeliae*) and the Cassin's auklet (*Ptychoramphus aleuticus*). Cormorants (Phalacrocoracidae) were the most commonly misclassified pursuit diver. Cormorants were plotted near other plunge diving birds. A few plunge divers were ambiguous in their classification grouping near pursuit divers these include: gannets, albatrosses, petrels, and frigatebirds.

DISCCUSION

Previous studies have found a difference in the morphology of eyes of nocturnal and diurnal non-aquatic birds (Hall 2008, Schmitz 2009), A difference in nocturnal and diurnal eye morphology is also present in aquatic birds. However, the eyes of cathemeral aquatic birds cannot be distinguished from diurnal aquatic birds. Deep diving species such as *Aptenodytes patagonicus* and *Aptenodytes forsteri* were never misclassified as nocturnal despite hunting for fish in the deep ocean with minimal illumination. In general, larger absolute eye size is more likely to be incorrectly classified with many of the owls not being classified as nocturnal. Most aquatic birds are classified as diurnal in the literature but frequently dive to depths in the ocean with light levels are similar to those experienced by cathemeral or nocturnal species on land. However neither a linear nor higher dimensional regression analysis were able classify aquatic birds to their correct dive depth using measurements of the orbit and scleral ring.

Neither the neural network nor regression analysis was able to recover a pattern in eye morphology that related to dive depth. This indicates that dive depth is not influencing the shape of scleral ring or orbit. The available data on dive depth is limited. Most of the dive depth information is obtained when the birds are breeding on land and are incubating eggs or rearing chicks. Activity during breeding may not be representative of how the birds feed throughout the year. Feeding young increase the energetic requirements for birds, especially in pursuit diving birds (Roby & Ricklef 1986, Cairnes 1988). In some species, alcids and penguins, the birds will make shallow nocturnal dives during breeding season in order to feed both themselves and their chicks (Burger 1993, Gaston 1998, Moore 1999). There can also be significant variance in the maximum dive depth within a species based on geographic location. There can be up to a 20 meter difference in the maximum dive depth and a 10 meter difference in mean dive depth between two colonies of Magellanic Penguins within the same year (Scolaro & Suburo 1991). Some of this variation may be a result of where prey are located in the water column .The wide variation in energy expenditure and depth of prey capture in aquatic birds probably contributes to the inability to determine a specific eye morphology related to dive depth.

Nocturnal animals optimize for greater sensitivity at the expense of acuity though an increase in the pupil diameter (INT) and reduction in posterior nodal distance (OL) producing a brighter image on the retina (Land 1981, Schmitz 2010). In aquatic birds, there are multiple methods of altering the eye to make it more suited to an aquatic environment but not all birds adopt the same mechanisms. Penguins have a flattened

cornea to reduce loss of resolution when entering the water and a flexible crystalline lens to accommodate their vision underwater (Sivak 1977, Martin 1985). Mergansers and Cormorants retain corneal curvature but use a strong flattened iris sphincter muscle to form a lenticonus through the pupil (Sivak 1980). These changes in soft tissue of the cornea and iris muscle may not be as obvious in the hard tissue of the orbit and scleral ring.

While penguins have the largest ratio between the INT and EXT ring diameter which is most usually associated with nocturnal animals; penguins were not classified as more similar to nocturnal birds and dive depth did not seem to impact eye shape classification. Penguin scleral ring shape is relatively similar across the clade despite dive depths ranging from 60 to 265 meters (Appendix B). Alcids have deep diving species, *Uria lomvia*, that while diving to depths 2-3 times greater than closely related taxa, show no significant difference in scleral ring or orbit shape.

Dive style (pursuit, plunge, surface seizure, or dipping) is able to be classified with only a few errors. The misclassified species often species utilizing multiple dive styles and tend to group correctly within their range of styles. The albatross is mainly a surface-seizer in dive style but also performs pursuit-plunge dives for a short distance into the water (Prince 1994), which may explain the black-browed albatross falling within the pursuit diving range. Misclassified birds are at the periphery of the classification line, which is expected when they have multiple dive styles. This regression analysis was not weighted for phylogenetic relationships because Pagel's

lambda values were all below .000005 for all of the orbit and scleral ring measurements when log transformed to account for the affect of body size.

CONCLUSIONS

The waterbird clade and Charadriiformes include birds that occupy a diverse spectrum of environments from shallow water skimmers to deep divers operating at the absolute threshold of illumination for the eye. Many of these diving birds must also use their eyes while on land to find a nest or a mate and to avoid predators. Despite the change in light attenuation in the ocean depths where some of these taxa forage the morphology of the scleral ring is best classified by the time of day when the bird is active not the dive depth.

The depth to which aquatic birds are diving does not result in significant changes to the scleral ring. This is probably due to the variability of dive depth between individuals based on water depth, location of prey, and time of year. Additionally, in most studies the number of individuals with recovered records is usually fewer than half of the birds tagged with recorders with some studies having sample sizes as low as two individuals. Additionally, the short amount of time the birds spend at these depths, usually less than one minute, may not be sufficient to result in detectable changes to the shape of the boney tissue of the orbit and scleral ring.

However, dive style does seem to influence the shape of the scleral ring and eye. How a bird enters the water and how long it is submerged looking for food are more consistent then the depth to which the bird are diving. Birds with multiple dive styles fall

between the classes reflecting different pressures on the morphology of the eye to optimize for multiple dive styles. Several species such as gannets and alcids have unusual scleral ring morphologies that could reveal novel mechanisms for accommodation.

Chapter 2: Qualitative characters of the scleral ring in aquatic birds

The morphology of the scleral ring has been related to dive depth and activity pattern in fish and has been shown to have phylogenetic signal in lizards and birds. In this study, the number of ossicles and other descriptive characters of the scleral ring: ossicle overlap, the morphology of the edges of the ring, and nature of contact among ossicles of the ring are evaluated for two major clades of birds, a well-supported waterbird clade (including Sphensciformes, Procellariiformes, "Pelicaniiformes" and Ciconiiformes) and shorebirds (Charadriiformes). Specifically the degree to which these discrete characters of the ring may show a relationship with ecological variables such as dive depth or prey capture method is evaluated.

Ossicle number is the most frequently discussed character of the scleral ring in studies of fish, lizards, and birds. In this study, modal ossicle number was measured for 87 avian species. Phylogenetic signal in modal ossicle number by clade was evaluated using Pagel's lambda. Both the waterbird clade and Charadriiformes show Pagel's lambda values close to 1, a value of .96 in waterbirds and .93 in Charadriiformes, indicating strong phylogenetic signal in this character. Within the waterbird clade, there was a range in ossicle number from a high of 16 ossicles in cormorants (e.g. *Phalacrocorax)* to a low of 10 ossicles in sulids (boobies and gannets). A decrease in ossicle number is observed within Spheniscifomes. The largest taxa, in *Aptenodytes*, have 15 ossicles and the smallest species, *Eudyptula*, has only 12. A morphology of ring overlap and scalloping is present mainly in alcids (auks and puffins) and the

monophyletic core of “Pelecaniformes”. Puffins show an unusual concentration of extreme internal ring serrations and ossicle overlap not found in any other birds.

INTRODUCTION

The avian scleral ring is a ring of small plate-like bones located in the corneal hemisphere of the eye (Walls 1942, Hall 1981, Martin 1985, Warheit 1989). The individual plates that form the scleral ring, ossicles, overlap in an imbricating pattern with one edge above and one below the neighboring ossicles (Figure 9). The scleral ring is hypothesized to function in two ways: The first being for the support and protection of the eye at the corneoscleral junction; the second as an anchor point for the ciliary muscles of the eye (Lemmrich 1931, Curtis & Miller 1939, Walls 1942, Martin 1985). The ciliary muscles do not attach directly to the scleral ring but insert into the sclera on the inside of the bony ring.

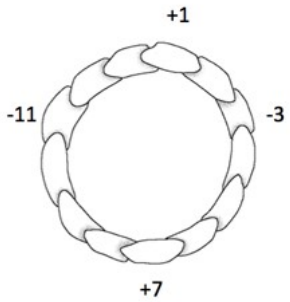


Figure 9. Pattern of imbrications on a scleral ring

The pattern of overlapping and underlapping ossicles in the scleral ring of *Uria lomvia*. Overlapping ossicles are designated as “+” and underlapping ossicles as “-“. Ossicles with normal (one side overlapping and one side underlapping) imbrications are unmarked. The pattern in this ring is +1, -3, +7, -11.

The distribution of scleral elements, both the ossicles and cartilage, is variable among vertebrates. A cartilaginous scleral cup is present in chondrichthyans, amphibians, turtles, lizards, crocodylians, and birds. Scleral ossicles are present in basal fish such as acanthodes but seem to be lost early on and subsequently regained in some derived teleosts (Forey & Young 1985, Franz-Odendaal & Viacaryous 2006). Scleral ossicles are broadly distributed in basal amniotes, present in lepidosaurs, basal archosaurs and are retained in all avian and non-avian dinosaurs. They are likely plesiomorphic for Amniota and are secondarily lost in some crocodylian-line archosaurs, snakes and mammals (Underwood 1970, Caprette et al. 2004, Nesbitt et al. 2012). However, it should be noted that given that the induction of the individual scleral ossicles in distinct groups of teleost fishes, lepidosaurs and birds occurs in a slightly different manner questions have been raised concerning their homology (Franz-Odendaal 2005, Franz-Odendaal & Hall 2006).

Scleral ossicles develop through cartilaginous replacement in teleosts and other fish (Franz-Odendaal & Vickaryous 2006). In tetrapods, scleral ossicle are neural crest derived bone induced through an epithylial-mesenchymal interaction separate from the scleral cartilage (Creuzet et al. 2005, Franz-Odendaal & Vickaryous 2006). Avian ossicles, like the rest of Reptilia, are induced by transient scleral papillae with each papillae corresponding to an ossicle (Franz-Odendaal & Hall 2006, Franz-Odendaal 2008). Removal of a single papillae results in a loss of an ossicle but not a gap in the sclera ring. The neighboring ossicles enlarge to cover the resulting space in the ring (Coulombre et al. 1962). Cryptodiran turtle scleral elements are derived

intramembranously in a manner more similar to lizards and birds, however the transient scleral papillae are not as distinct (Franz-Odendaal 2005). Here, prior studies of the osseous adult structures are reviewed despite these recognized differences in their development.

Modal scleral ossicle number has been the most commonly evaluated characteristic of the scleral ring (Lemmrich 1931, Curtis & Miller 1939, de Queiroz & Good 1988, Warheit et al. 1989, Lima 2009). Lizards and birds both typically have a range of 10 – 16 ossicles per eye (de Queiroz 1982, de Queiroz & Good 1998, Franz-Odendaal & Hall 2006). In both of these groups, the number of ossicles is known to vary among distinct subclades (Lemmrich 1931 Warheit et al. 1989, Queiroz and Good 1998). De Queiroz and Good (1998) used parsimony-based ancestral state reconstruction of ossicle number to argue for the phylogenetic placement of a controversial bird species, *Opisthocomus*, with Cuculiformes rather than Galliformes. The Warheit et al (1998) study noted a decreasing trend in ossicle number within "pelecaniform" birds with sulids (boobies and gannets) having the fewest ossicles in the ring of any measured species in that clade. More recently, Lima (2009) focused on Brazilian birds and found both variation by subclade as well as individual right/left differences in the number of ossicles. All studies of this character system have agreed that modal ossicle number is influenced by phylogeny and occasionally note some variation in other qualitative characters of the ring such as overlap or thickness (Lemmrich 1931, Curtis & Miller 1939, de Queiroz & Good 1988, Warheit et al. 1989, Lima 2009) but none systematically evaluate multiple qualitative characters of the scleral ring for phylogenetic or ecological signal.

Recent studies by Schmitz and Motani (2010) and Hall (2008) have found that measurements of the diameter of the scleral ring and orbit correlate with optical properties of the eye but did not consider discrete characters of the ring such as number. Changes in the ratio of the scleral ring and orbit are correlated to activity pattern with extremely nocturnal and diurnal activity patterns being easiest to classify using the skeletal material alone. Variation in the shape of individual ossicles as well as the thickness of the ring has been recorded for some birds but has not been evaluated for phylogenetic or ecological signal (Curtis & Miller 1939). In general, passerine birds have more fragile thin rings while the thickest rings were reported in larger predatory birds such as the great horned owl (*Bubo virginianus*) and diving birds (Curtis & Miller 1939).

In this study, qualitative characters of the ring including the modal ossicle number, shape, overlap, and serration of the ossicles are evaluated to look for phylogenetic signal and to investigate if these qualitative characters are influenced by ecological factors such as dive style or dive depth.

Another character evaluated in previous studies is the pattern of ossicle overlap (Figure 9). This pattern of ossicle overlap is conserved at the ordinal level of lizards but there is species and genera level variation within these clades (de Queiroz 1982). However, there seems to be more variation in pattern within bird species (Warheit et al. 1989). In this study, as many as five of these previously described patterns were found within a single taxon with the pattern occasionally varying between eyes in a single specimen. The high variability in this character indicates it may not have a strong phylogenetic signal and was not evaluated as such.

This study will expand the taxonomic breadth of the Warheit et al. (1989) study to include all of the waterbird clade (Clade H) as identified by Hackett et al. (2008) and shorebirds (Charadriiformes) as identified by Smith (2011). Including all of the waterbird clade samples a more diverse range of ecologies, such as Sphenisciformes (penguins), a group of wing-propelled pursuit divers that have the deepest diving aquatic bird, *Aptenodytes patagonicus*. The sister clade to Sphenisciformes, Procellariiformes, consisting of Diomedeidae (albatrosses), Procellaridae (shearwaters and petrels), Hydrobatidae (storm petrels) and Pelecanoididae (diving petrels); mainly shallow divers utilizing surface seizing, surface dipping and occasionally plunge diving to acquire prey (del Hoyo et al. 1996). The waterbird clade also includes mainly non-diving groups like Ciconiiformes (herons, ibises, hammerkop and pelicans). These taxa are mainly waders that utilize their bills to scoop or spear prey (del Hoyo et al, 1996) with the notable exception of pelicans. Charadriiformes, shorebirds, while not closely related to the waterbird clade, also includes species with a diversity of dive styles and dive depths. This group includes Alcidae (murres, auks, razorbills and puffins), mainly wing propelled pursuit divers some of which are capable of reaching dive depths similar to those of much larger penguin species (Gaston et al. 1998). The sister group to Alcidae, Stercorariidae (skuas), are a non-diving opportunistic feeder often relying mainly on kleptoparasitism during breeding seasons by stealing from gulls, terns, and other seabirds (del Hoyo et al. 1996). There is also a large array of more terrestrial foraging taxa within Charadriiformes, including Glareolidae (coursers and pratincoles), Scolopacidae (sandpipers and curlews), and Charadii (plovers). The only other group besides Alcidae

that dives for prey in Charadriiformes is Laridae (gulls) with some species utilizing plunge diving to capture prey (del Hoyo et al. 1996).

Evaluating multiple clades with diverse ecologies will increase the ability to determine if qualitative characters of the scleral ring vary with changes in dive depth and dive style. An increase in ossicle thickness and number occurs in more "active" fish to stabilize the eye against greater pressure associated with faster movement (Franz-Odendaal 2008). It is possible that a similar increase in rigidity might be seen more actively diving birds that forage underwater where the eye is subjected to greater pressure. The birds in this study are foraging at different speeds and experiencing different amounts of water pressure as a result of different dive styles and dive depths. For example, sulids, fast aerial plunge divers, have a reduced number of ossicles compared to surface diving Phalacrocoracidae (Warheit et al. 1989). Sulids impact the water from a steep aerial dive putting pressure on the eye while cormorants dive from the surface, reaching a greater depth but without the sudden force of impact.

Sphenisciformes are wing-propelled deep ocean divers with the Emperor Penguin diving to depths of over 250 meters at a velocity of 3 m s^{-1} (Kooyman 1972, 1992). In this study, changes in ossicle number within deep diving clades such as Sphenisciformes and alcids are evaluated against closely related shallower divers such as Diomedidae and Laridae to determine how ossicle number varies in relation to dive depth. Additionally, the amount of ossicle overlap, serration, and scalloping will be compared amongst diving and non-diving groups to see if diving ecology influences these characters.

MATERIALS

Data were collected from both the right and left scleral ring of 317 specimens from 87 non-passerine bird species (Illustration A, Appendix D). Taxonomic sampling includes 38 species of Charadriifromes. All major clades were represented; 22 species from Alcidae (auks, razorbills, murres, auklets and puffins), 1 species from Stercorariidae (skuas), 5 species from Laridae (gulls), 5 species from Ternidae (terns), 2 species from Glareolidae (coursers and pratincoles), 2 species from Scolopacidae (sandpipers and curlews) , and 2 species from Chardrii (Plovers). Taxonomic sampling with in the waterbird clade (Clade H) included 52 species. A total of 13 species from "Pelecaniformes" (boobies, gannets, and cormorants) , 8 species from Ciconiiformes (herons and ibises as well as pelicans), 13 species from Procellariformes, 10 species from Sphenisciformes (penguins), 4 species from Gaviiformes(loons), and 2 species from Musophagiformes (turacos). Specimens were obtained from The American Museum of Natural History (New York), United States Museum of Natural History (Washington D.C), The Burke Museum (Seattle), Texas Memorial Museum (Austin). Specimen numbers are given in Appendix A .

METHODS

Five qualitative characters of the scleral ring were evaluated: total number of ossicles, amount of ossicle overlap, presence of interwoven ossicles, presence of scalloping on the internal and external edges of the ring, and the presence of serrations on the internal and external edges of the ring (Figure 10, Appendix D). All rings were evaluated from skeletonized museum specimens; no rings were evaluated in situ. As a result, the siding

of ossicles was inferred based on the shape and pattern of ossicle overlap. Ossicles tend to be widest at the temporal dorsal edge and slightly asymmetrical nasally (De Quiroz and Good 1988). The pattern in scleral ossicles was evaluated using the method developed by Lemmrich (1931) (Figure 9). Plates that overlap the adjacent ossicles on both sides are designated as overplates with a positive "+" and plates that are underlapping the adjacent ossicles on both sides are designated as underplates "-". The ventral most overlapping ossicle is designated as number one and ossicles are counted up the temporal side and down the nasal side of the ring (Lemmrich 1931, De Quiroz and Good 1988). A notable exception to the imbricating overlap pattern are the presence of ossicles that form an "S" like shape at the boundary with a portion of the ossicle both overlapping and underlapping the neighboring plate (Figure 10 B). The presence of "S" shaped interlocking ossicles are also seen in lizards in which case the corneal most overlap is counted when determining the pattern of overlap. The "S" shaped or interlocking ossicles were not observed in all species but were noted when they did occur. Interlocking ossicles are scored as 0 if there are no interlocking ossicles present in any of the specimens.

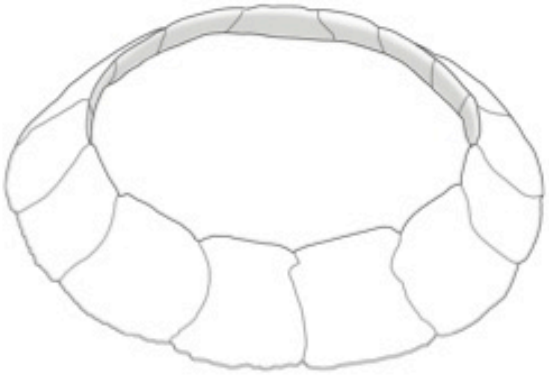
A Ossicle Overlap

0. Minimal overlap
Sula dactylatra
USNM 498030

1. Modeate overlap
Uria aalge
USNM 623292

2. Extreme overlap
Fratercula cirrhata
USNM 556448

B Interolocking Ossicles



0. Absent
Aptenodytes forsteri
USNM 553580

1. Present
Cepphus colomba
USNM 612988

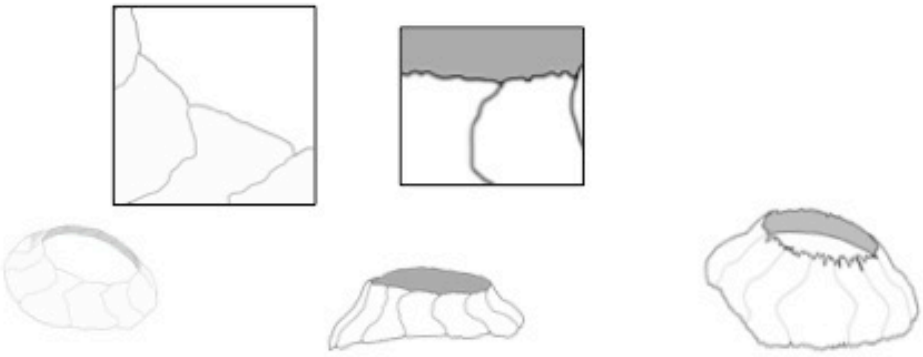
5mm

C Reduced Ossicle

0. Absent
Ardea herodius
UWBM 18618

1. Present
Uria lomvia
USNM 502367

D Internal Serrations



0. Absent
Alca torda
USNM 502382

1. Present – moderate
Sterna maxima
UWBM 45817

2. Present – extreme
Fratercula cirrhata
USNM 556448

5mm

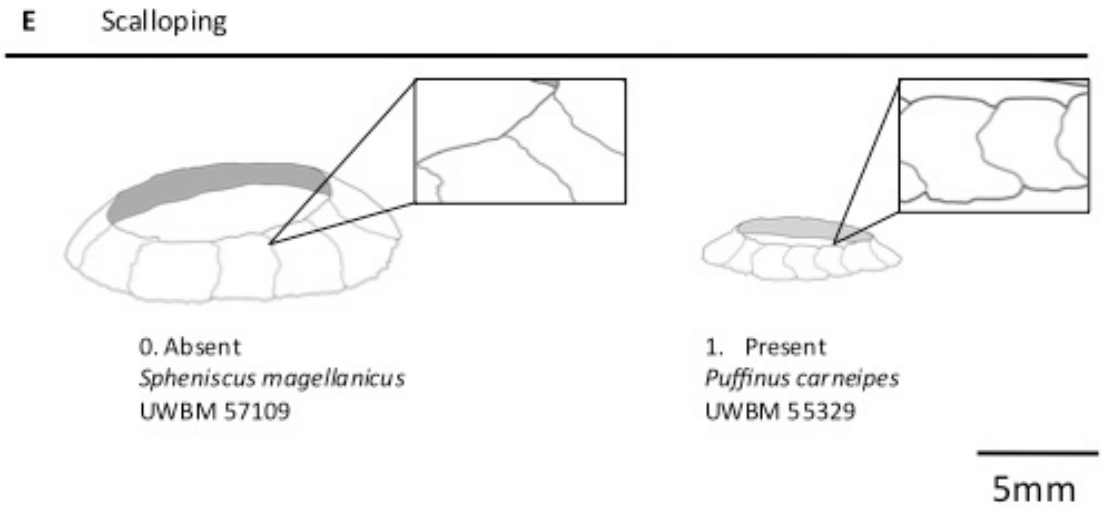


Figure 10. Illustrated characters of the scleral ring

A Overlap between neighboring ossicles. A three state character with minimal overlap of less than a quarter of the ossicle, moderate overlap at less than half of the ossicle, and extreme overlap with one half or more overlap of the ossicle. **B** Interlocking ossicles. A three state character where a single ossicle both overlaps and is overlapped by its neighboring ossicle on a single side forming an "S" shaped connection. **C** Reduced ossicles. These ossicles are usually less than half the size of the rest of the ossicles in the ring. **D** Internal serrations. A three state character describing the texture along the internal margin of the ring. The margin can be smooth, have minimal serration, or extreme finger-like serrations. **E** Scalloping. The presence of a pattern of rounded edges followed by sharply indented clefts along the margin of the ring.

A score of 1 indicates at least one ring showed one interlocked ossicle. If more than two specimens had interlocked ossicles a score of 2 was assigned to that taxon. Scalloping is the presence of regular rounded protrusions followed by steep indentations along the margin of the scleral ring. These indentations are usually at the meeting point of two ossicles and the amount of protrusion is influenced largely by the shape of the individual ossicles. A score of 0 indicated the edge is smooth. A score of 1 indicates the

presence of scallops (Figure 10 E) . Serrations are the presence of bumps and ridges on the margins of the ring. A score of 0 indicates a smooth surface. A score of 1 indicates small ridges were present. A score of 2 is given when the serrations are exceptionally long, forming finger-like projections (Figure 10 D). Finally, ossicle overlap is the degree of overlap between neighboring ossicles. This character was only evaluated at the normally imbricating ossicles of the ring. The overlapping and under lapping ossicles often had different overlapping patterns from the rest of the ring and were not considered in scoring. A score of 0 is minimal overlap with less than a quarter of the ossicle covered by the neighboring plate. A score of 1 is for overlap covering a quarter to a half of the ossicle. A score of 2 is given to any ossicle with an overlap of one half or greater (Figure 10 A).

All character score were recorded in Mesquite version 2.75 (Maddison & Maddison 2011). Ancestral states were reconstructed for a supertree that takes the Hackett et al. (2008) topology as its base. As the relationships among species sampled here were not investigated in that analysis, placement of these taxa was based on phylogenies from the following studies: McCracken and Sheldon 1998, Nunn and Stanley 1998, Kennedy et al 2000, Hackett et al 2008, Kspeka and Clarke 2010. A separate tree was constructed for Charadriiformes based on the phylogeny from the study by Smith (2011). All of the characters appear to be morphoclines (e.g., small, medium, large degrees of overlap), they were mapped as ordered (Slowinski 1993). Reconstruction of ancestral states was based on parsimony and maximum likelihood and was undertaken in Mesquite version 2.75 (Maddison & Maddison 2011). Phylogenetic signal was measured

using Pagel's lambda (Pagel 1999). This test statistic gradually removes phylogenetic structure to determine how much of the variation is reflected by a shared evolutionary history, a value of 1 indicates phylogeny explains all of the variation and a value of 0 indicates none of the variation is explained by the phylogeny. These values were computed for a set of branch lengths utilized for the waterbird clade (Clade H of Hackett et al. 2008) from Xia and Clarke (2014) and from Baker et al. (2007) for Charadriiformes on a tree from Smith (2011). Dive depth and prey capture for available species was taken from the literature (Appendix C) and evaluated relative to ossicle characters.

RESULTS

Ossicle Number

The total number of ossicles for both Charadriiformes and water birds (Clade H of Hackett et al., 2008) ranged between 10 and 17 in agreement with the most common values found in the Lemmrich (1931) study. Most species in both groups had a modal number between 14 and 15 (Figure 11). Fourteen was reconstructed as ancestral for both of the Charadriiformes and waterbirds using parsimony. However maximum likelihood found all numbers equally likely for waterbirds and 14 or 15 equally likely for Charadriiformes (Figure 12). A reduction in number was present in core "Pelecaniformes" (excluding *Pelecanus*) with modal number dropping to 12 and 13 ossicles in the common ancestor of Anhingidae and Phalacrocoracidae. One part of this clade, boobies, in the genus *Sula* had the lowest modal ossicle number of all measured species with a modal number of 10 ossicles per ring. A modal number of 14 – 15 ossicles was observed in all ciconiforms with the exception of *Pelecanus*; none of these birds

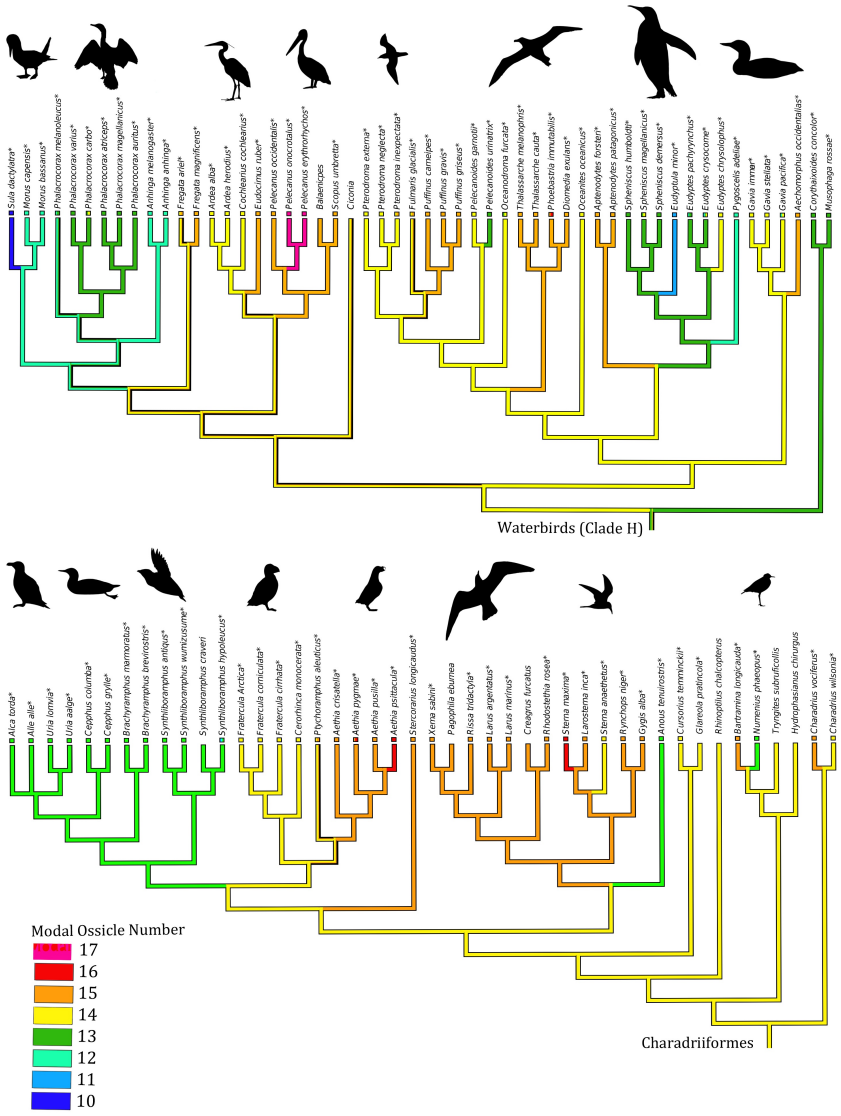


Figure 11. Parsimony modal ossicle number reconstruction

Parsimony reconstruction of modal ossicle number as a heat map with the higher number of ossicles representing warmer colors and the lower number of ossicles the cooler numbers.

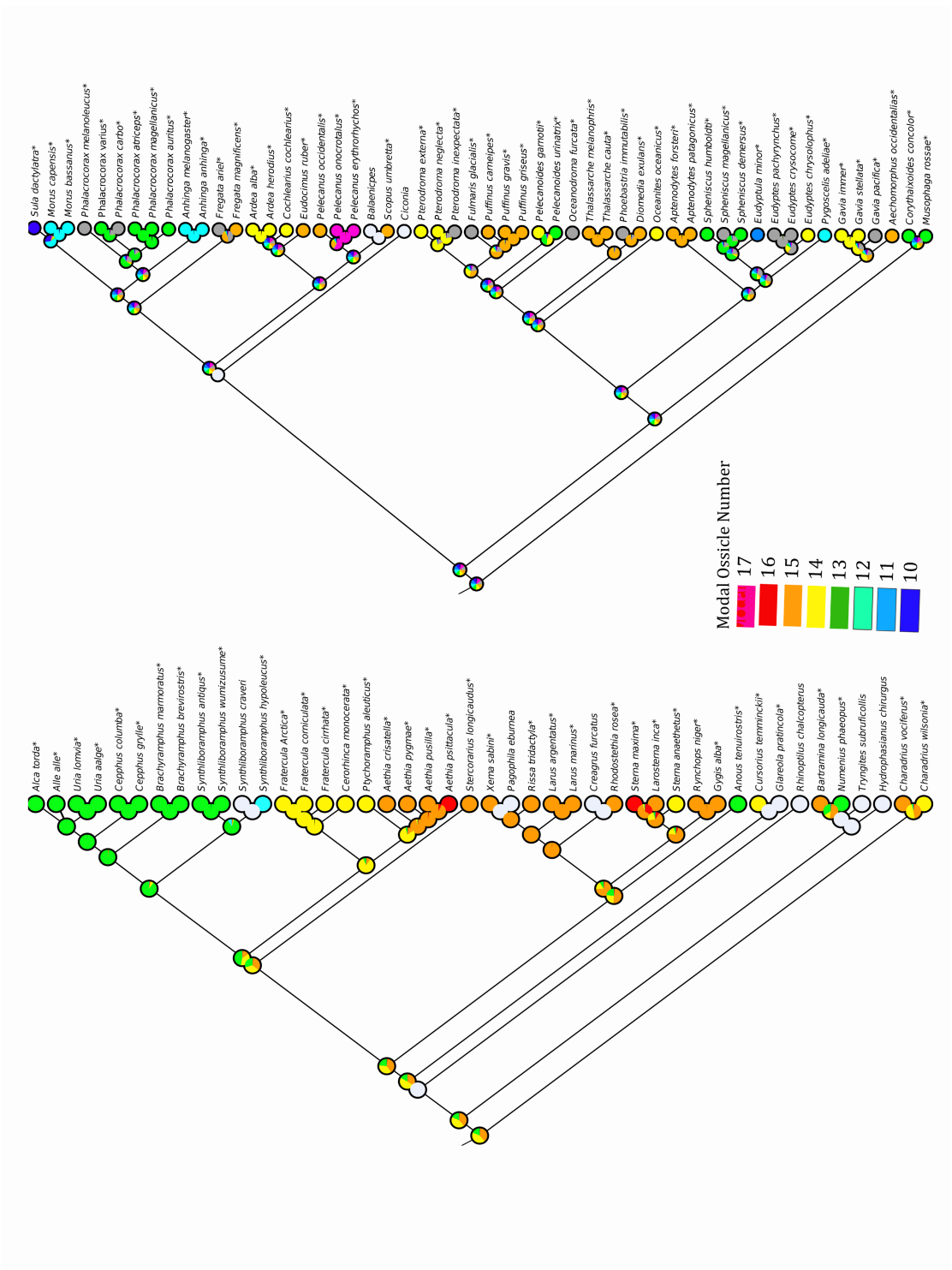


Figure 12. Maximum likelihood modal ossicle number reconstruction

Modal ossicle number reconstruction using maximum likelihood. Waterbirds are shown at the top and Charadriiformes at the bottom. Higher ossicle numbers are in warmer colors and lower ossicle numbers are in cooler colors Gray circles indicate a polymorphic trait.

dive, most use their bill to probe for fish, crustaceans, or insects while wading near the shore (del Hoyo et al. 1996). The largest number of ossicles of all waterbirds was in pelicans with a modal number of 17 in *Pelecanus onocrotalus* and *Pelecanus erythrorhychos*. Both *Pelecanus onocrotalus* and *Pelecanus erythrorhychos* are large (20 - 25lb) birds that sit on the surface of the water dipping their bill into the water to scoop up prey but neither species dive. *Pelecanus occidentalis* has a modal number of 15 ossicles and is much smaller (6-12lbs) and will fly over the water before plunge diving to capture prey (del Hoyo et al. 1996).

Within the waterbird clade Penguins show a decrease in ossicle number over the ancestrally reconstructed condition of 14. One of the most basal divergences within Sphenisciformes, *Aptenodytes*, have a modal number of 15 ossicles. This group also has the greatest total number of ossicles in one ring observed in penguins, 16, in *Aptenodytes foresteri*. However, *Aptenodytes foresteri* also had wider variation in ossicle number, one specimen, AMNH 3600, had only 13 rings in each eye. The variation in ossicle number is not a result of ontogenetic stage, as the number of ossicles is fixed prior to hatching with plates growing in size but not in number (Wall 1942, Hall 1981, Franz-Odendaal 2008). The modal ossicle number drops to 12 in the *Spheniscus* clade of penguins and was lowest in the little blue penguin, *Eudyptula minor*, with only 11 ossicles. The decrease in ossicle number also parallels a decrease in dive depth with *Spheniscus* penguins having a

maximum diving depth of less than 100 meters and *Eudyptula minor* diving a maximum of only 27 meters (Appendix C).

Charadriiformes show less variation in modal ossicle number compared with waterbirds; a range from 13 to 16 ossicles is observed in the clade (Figure 12 & 13). Within Alcidae there is reduction from an estimated ancestral 14 ossicles to 13 in Alcinae (murres, guillemots, murrelets, and razorbills) and an increase to 15 ossicles in *Aethia* (auklets). This increase in ossicle number occurs in the shallowest alcid diving species, *Aethia*, with maximum dive depths of 20 meters or less with the exception of *Ptychoramphus aleuticus,* which has a maximum dive depth of 28 meters (Burger & Powell 1990, Gaston & Jones 1998). Most auklets have a range of ossicle number between 14 and 16. A majority of the measured *Aethia* species had 15 ossicles. The sister clade to Aethia, Fraterculini, has a modal ossicle number of 14 but taxa in this clade also dive slightly deeper with most species having a maximum dive depth of 50 meters (Burger et al. 1993).

The lowest number of ossicles in Alcidae occur in the murres, *Uria lomvia* and *Uria aalgae*, with one individual in *Uria aalge* having only 10 ossicles in both scleral rings and two individuals in *Uria lomvia* having only 12 ossicles in each scleral ring. Murres are some of the deepest divers within Charadriiformes; the maximum recorded dive depth for both species of Murres is over 100 meters, deeper than some members of the *Spheniscidae* clade of much larger size (Croll et al. 1992, Gaston & Burger 1998).

Charadriiformes are ancestrally reconstructed as having a modal number of 14 or 15 ossicles. Laridae (gulls) includes several species, *Larus argentatus* and *Larus marinus*,

with individuals having up to 16 ossicles. Both *Larus argentatus* and *Larus marinus* are larger gulls that are mainly opportunistic feeders and infrequently make dives of a little more than 1-2 meters in pursuit of prey (del Hoyo et al. 1996). The only reductions within this clade occur in *Anous tenuirostris* (Lesser Noddy) and *Numenius phaeopus* (Whimbrel) both with a modal number of 12 ossicles. Neither bird dives.*Anous tenuirostris* is a smaller surface feeder and *Numenius phaeopus* is a terrestrial or littoral forager that uses a long curved bill to pull larvae and crustaceans from the ground (del Hoyo et al. 1996).

Overlap

All but four species of waterbirds have moderate overlap between adjacent ossicles, score 1, where about one quarter of the ossicles sits over its neighbor (Figure 13). The exceptions being Sulidae, which has almost no overlap between adjacent ossicles, with an overlap score of 0. Sulidae was the only group with this score in either the waterbird or Charadriiform clades. At the opposite extreme within waterbirds, *Ardea alba* has a strong overlap, with a score of 2. *Ardea alba* does not dive and usually spears food with its long sharp beak while wading in shallow waters less than 20 cm deep (del Hoyo et al. 1996). A similar prey capture method is employed by the closely related *Ardea herodius* that has moderate ossicle overlap like all other Ciconiiformes.

Overlap is moderate for most species within Charadriiformes. Exceptions occur within *Brachyramphus, Aethia* (aukles) and Fraterculini (puffins). *Brachyramphus* is the

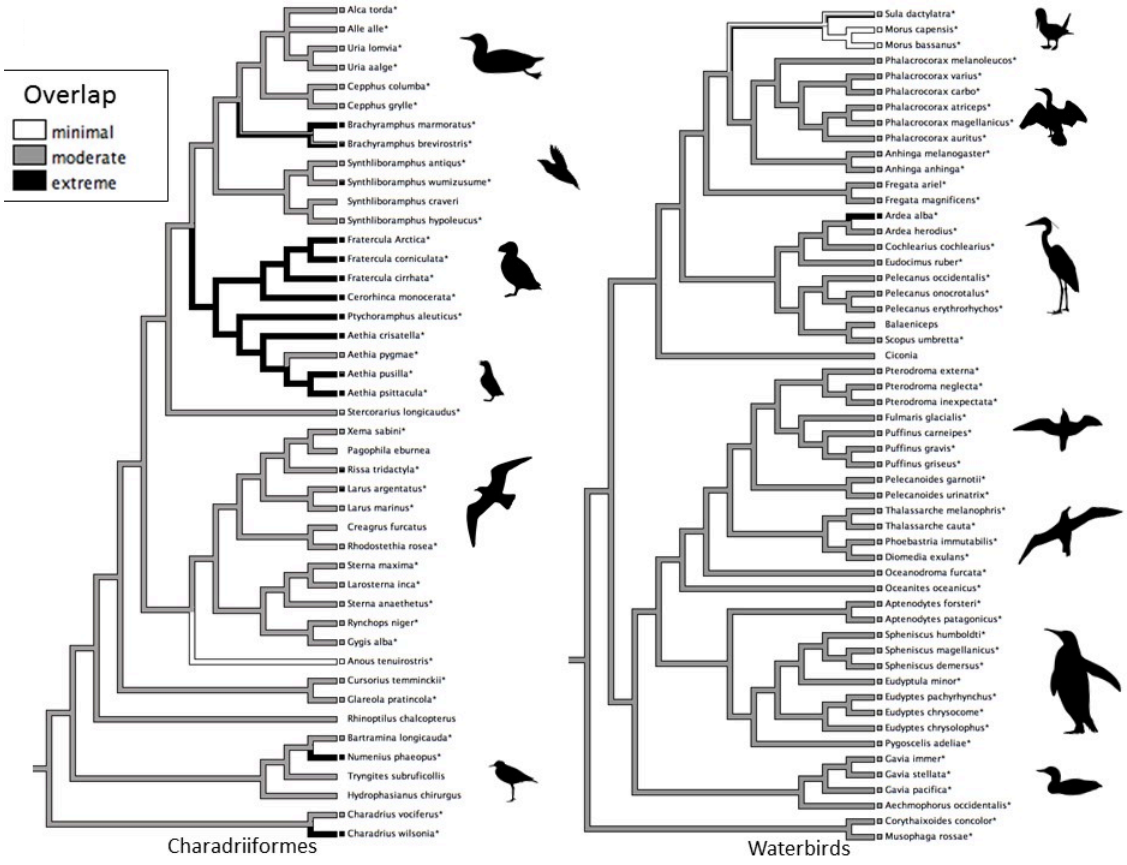


Figure 13. Ossicle overlap parsimony reconstruction

Parsimony reconstruction of ossicle overlap in Charadriiformes and waterbirds. Darker colors indicate a higher degree of overlap. Most of the extreme overlap is concentrated in Fraterculini.

only member of Alcinae to have increased overlap. *Aethia* and Fraterculini are sister clades and both show an increase in overlap. Fraterculini (puffins) are the only wing-propelled diver to have all members scored as 2. In *Fratercula cirrhata* the overlap was so great that the edges of two non-neighboring ossicles contacted (Figure 2 A). Increased overlap increases the thickness of the ring making it more rigid and better able to resist deformation from increased water pressure while diving (Curtis & Miller 1939).

All of the measured species of *Aethia* except *Aethia pygmaea* have strong overlap. *Aethia pygmaea* has moderate overlap but is also a pursuit diver (Gaston & Jones 1998) Much like puffins; auklets are pursuit divers foraging on euphasiids on the ocean floor (Jones 1993).

Scalloping & Serrations

The presence of scalloping both on the interior and exterior edges of the scleral ring is scattered randomly throughout water birds and Charadriiformes. External serrations are present in most of the evaluated taxa. Internal serrations are also present in most of the evaluated taxa with a concentration of serrations in alcids (Figure 14). The most extreme example of both the internal and external serrations occurs in Fraterculini. The unusually long serrations on the internal edge of the puffin scleral ring had been noted in an earlier study (Smith 2011).

Interlocking ossicles

Interlocking ossicles occur in a small number waterbirds and are most common in the pelecaniform + ciconiform clade (Figure 14). All measured species of cormorants have interlocking ossicles with cormorants (e.g., *Phalacrocorax. carbo, Phalacrocorax atriceps*, and *Phalacrocorax auritus*) having multiple interlocking ossicles in a single specimen. Loons, Gavidae, also showed a remarkable amount of interlocking ossicles with *Gavia immer* and *Gavia stellata* having multiple interlocking ossicles, but none were observed in *Gavia pacifica*.

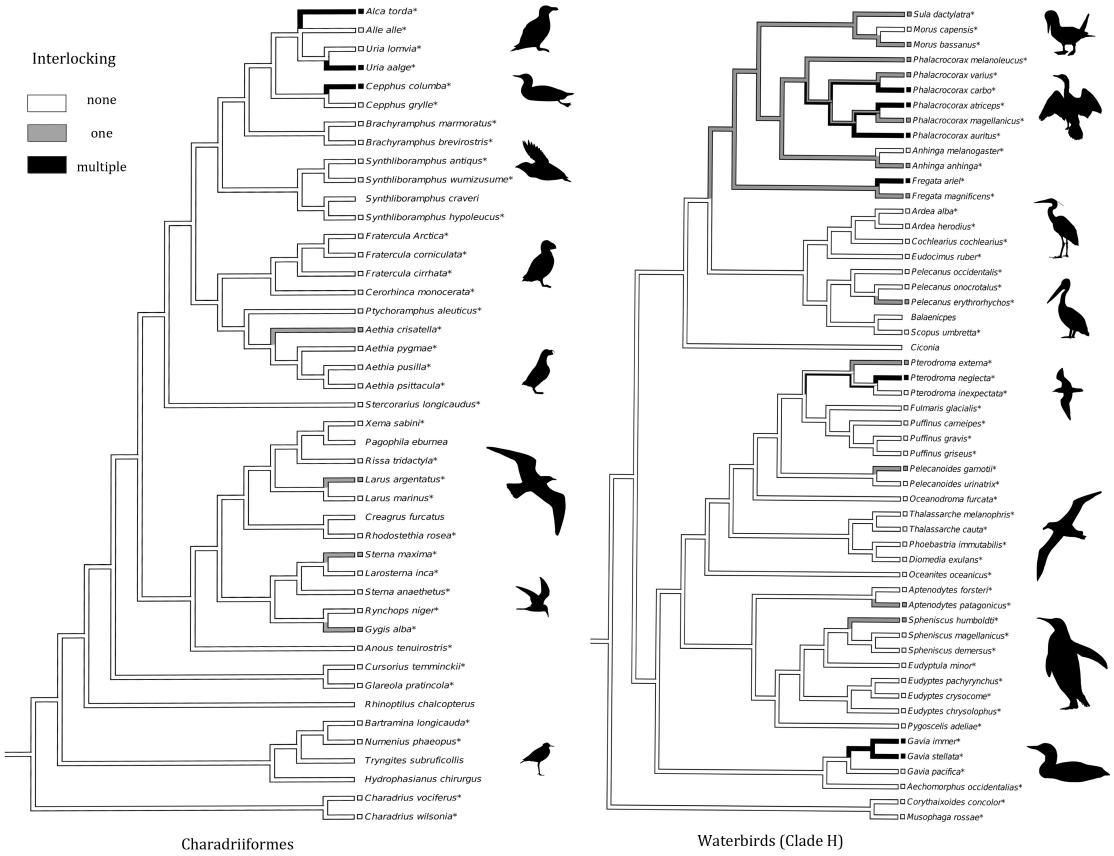


Figure 14. Interlocking ossicles parsimony reconstruction

Presence of interlocking ossicles in Charadriiformes and waterbirds. Ossicle interlocking is concentrated in cormorants and sulids.

Within Procellariformes several species have interlocking ossicles in their rings with the largest concentration in petrels: *Pterodroma externa*, *Pterodroma neglecta,* and *Pelecanoides garnotii*. Storm-petrels are pursuit divers with average dive depths around 20 meters but *Pelecanoides garnotii* has been recorded as diving up to 85 meters and is the only species of diving petrel with interwoven ossicles (Prince & Jones 1992, Jahncke & Zavalaga 1997). *Aptenodytes patagonicus* and *Spheniscus humboldti* are the only

penguins with interlocking ossicles. *Aptenodytes patagonicus* has a maximum dive of 256m while *Spheniscus humboldti* dive a maximum of 52 meters, neither species are the deepest divers within penguins, and *Spheniscus humboldti* is not a deep diver for its body size (Kooyman et al. 1992, Luna-Jorquera & Culik 1999).

Within Charadriiformes, the greatest number of species with interlocking ossicles was Alcidae, with the highest concentration in the groups with the deepest divers, murres (*Uria aalge*); razorbills, (*Alca torda*)*;* as well as the deepest diving guillemot (*Cepphus columba*), which can dive to depths of 45 meters (Ewins 1993). Interlocking ossicles were also present in one gull, *Larus argentatus*, a large gull that uses surface plunge diving to capture prey in dives (del Hoyo et al. 1996). Interlocking ossicles are also present in one tern, *Gygis alba*.

DISCUSSION

Scleral ossicle number has been evaluated for phylogenetic signal in birds, lizards and fish (De Queiroz 1982, Warheit et al. 1989, Franz-Odendaal 2006, Lima et al. 2009). Studies of lizard ossicle numbers show remarkable consistency in ossicle number within clades with some species level variation (Gugg 1939, Underwood 1970, De Queiroz 1982). The avian scleral ring shows greater variation of ossicle number than observed in lizards with many species having different ossicle numbers between the eyes of a single individual. The amount of recorded variation depends on the study with Curtis and Miller (1939) reporting 14% of individuals showing variation and the embryological study by Franz-Odendaal (2008) reporting variation between eyes in a single individual as high as 51% of the time. This study finds variation of one ossicle between eyes 30% of the

individual specimens and a variation of 2 ossicles in 1% of individuals. Despite this variation is ossicle number within individuals, avian scleral ossicle number shows strong phylogenetic signal within waterbirds and Charadriiformes, e.g. a high Pagel's lambda value of 0.96 indicating phylogeny explains most of the variation in this trait (Pagel 1999).

A decrease in ossicle number occurs within core "Pelecaniformes" (excluding *Pelecanus* but including boobies, gannets, cormorants and frigate birds) and within Sphenisciformes. Warheit et al. (1989) also recovered decreasing ossicle number from 14 to 13 in Phalacrocoracidae and from 13 to 12 in Sulidae. A final reduction to 10 ossicles occurs in *Sula* that show the smallest recorded number of ossicles in an avian species (Lemmrich 1931, Warheit et al 1989). The number of ossicles does not seem to be related to water pressure as seen in teleosts. Penguins are wing propelled pursuit divers, gannets make rapid plunge dives into the water from up to 10 meters in the air (Adams & Walter 1993), and murres and guillemots are the deepest divers within Charadriiformes; most of these species show a decrease in ossicle number over the ancestral condition. An exception is the increase in ossicle number in pursuit diving *Aethia* and *Aptenodytes* as well as large non-diving members of *Pelecanus*.

In addition to a decrease in ossicle number, diving groups like Spheniscidae, Sulidae, Alcinae tend to show an increase in interwoven ossicles and presence of reduced ossicles. Interwoven ossicles are most concentrated in Phalacrocoracidae, Sulidae, and three species of Alcids: *Alca torda, Uria aalge*, and *Cepphus columba*. A chi-squared test of independence supports a correlation between shallow and deep dive depths and an

increase in the presence of interlocked ossicles (Table 1). However, the test did not take into account phylogeny which could account for the non-random relationship between dive depth and interlocked ossicles. Cormorants are efficient predators of fish pursuing prey underwater using foot-propelled diving (del Hoyo et al. 1996). While Sulidae pluge dives from up to 10 meters in the air and unlike any other member of the waterbird clade have very little overlap between ossicles. An increase in interwoven ossicles could provide support for rings with otherwise minimal overlap allowing for fast plunges with minimal deformation of the eye. Similarly species using visual pursuit of prey underwater have a sturdier ring that could improve the stability of the eye against water pressure (Walls 1942, Curtis and Miller 1939).

The presence of reduced ossicles that sit on top of two normally imbricating ossicles are also observed in members of deep diving clades with reduced ossicle number: Sphenisciformes and Alcinae (Figure 10 C). *Spheniscus humboldti* and *Spheniscus magellanicus* had at least one individual with a reduced ossicle present on their scleral ring. Reduced ossicles have been hypothesized to be an intermediate state of ossicle loss in lizards (De Queiroz 1982). While homology among individual ossicles is difficult to determine, these ossicles tend to be present in bird species with reduced ossicle number where they overly adjacent ossicles. The distribution of these ossicles in deeper diving clades may be another mechanism for increasing contact between ossicles and stabilizing the scleral ring against the pressure of against water rushing over the eye as the birds dive. It occurs only in deeper diving groups with reduced ossicle number and never in shallower divers or non-diving species. Notably, reduced ossicles do not occur in

the deepest diving penguins, *Aptenodytes,* nor any Sphenisciformes other than *Spheniscus humboldti* and *Spheniscus magellanicus* . However, all penguins have a robust scleral ring with thick square shaped ossicles that increase the strength and rigidity of the ring. The ring in all penguins tends to be shorter in height with rectangular ossicles, none of the measured rings are elongate or tubular like those as seen in owls in contrast to the finds in the study by Lima et al. (2009).

Ossicle overlap is moderate across most species in both the waterbird clade and Charadriiformes. Notable exceptions include the plunge diving sulids, with reduced contact among ossicles, and the wing propelled diving puffins, with an unusually high degree of ossicle overlap. Indeed, in some puffins, two nonadjacent ossicles had edges that overlapped. No other measured species showed this degree of ossicle overlap. Strong overlap could be another means of increasing ring strength however puffin are not particularly deep divers and have a maximum dive depth of 60 meters and do not perform aerial dives.

External serrations seemed to be present in most species and do not show any distinct distribution based on clade. The presence of both internal and external serrations could be useful for increasing contact between the bony ring and the sclera in which it is embedded. A thickening of the scleral cartilage near the corneal edge of the scleral ring has been observed in penguins to increase rigidity of the eye (Scolaro & Suburo 1999). Internal serrations are concentrated in Fraterculini within Charadriiformes. The long finger-like serrations of puffins are one of many unusual features of their scleral ring and

could possibly be helping preserve the corneal curvature of the eye. Although why only this clade shows the feature is not known.

CONCLUSIONS

As previous studies have found (Curtis & Miller, 1938, De Quiroz & Good, 1988), the number of ossicles in the scleral ring is consistent within avian subclades and has strong phylogenetic signal. The variation in ossicle number seems to be concentrated in certain groups such as Sphenisciformes, but as sample sizes are low in that group increased sample size could recover a more consistent value for modal ossicle number (Appendix D). Additionally, there are some groups such as alcids where there is remarkable consistency in the ossicle number. Some of the consistency within Chardariiformes especially within plovers and sandpipers is probably a result of smaller sample sizes, 2-5 individuals, and should be investigated more thoroughly. However, dense sampling within Alcids recovered very little variation in ossicle number. Other traits such as scalloping show little variation in waterbirds and Charadriiformes and may indicate stabilizing selection.

Increased ossicle overlap, interlocking of ossicles, and the presence of reduced ossicles overlapping two other ossicles suggest changes to increase the overall strength and rigidity of the ring. These traits do tend to appear in faster, deeper divers such as penguins, plunge diving gannets, or deep diving murres (Figure 15). However, the unusual characters of the ring in Fraterculini does not seem correlated to dive depth or speed as they are not amongst the fastest or deepest divers (Kuroki et al. 2003, Watanuki et al. 2006). Similarly, higher frequencies of interwoven ossicles are seen in non-diving

taxa such as frigate birds. Frigate birds capture prey at the surface or steal fish from smaller birds while in the air (del Hoyo et al., 1996). The variety of ecologies showing overlap seems to provide evidence that overlap may not be related to only aquatic diving or prey capture. More extensive sampling within these groups could uncover more variation within the clades. Soft tissue dissection in species with unusual scleral rings like, puffins, could explain how the unusual morphology of their scleral ring relates to the optical performance of the eye. This study has documented more extensive variation in ring morphology than has been previously reported in Aves. It confirms phylogenetic signal in scleral ossicle number. Modified ring morphologies tend to be clustered in diving taxa but the modifications vary significantly across groups. For example, the exceptional modifications seen in puffins with internal serrations or the reduced interwoven and asymmetrical ring in most sulids are highly distinct from the thickened but little interwoven ossicles of penguins. Potential ecological or optical explanations of the observed patterns in discrete characters proposed here should be the subject of future inquiry.

Character	Chi Squared Value	Degrees of freedom	Probability
Interlocking	5.36	4	0.252
Internal Serrations	2.57	4	0.632
Overlap	11.7	8	0.167

Table 1: Chi squared values

Chi squared values for interlocking, internal serrations, and overlap evaluated against change in dive depth based on a binned value of shallow, medium, deep, or very deep diving. All three of these characters have a significant probability indicating that they changes in dive depth and each character are not random.

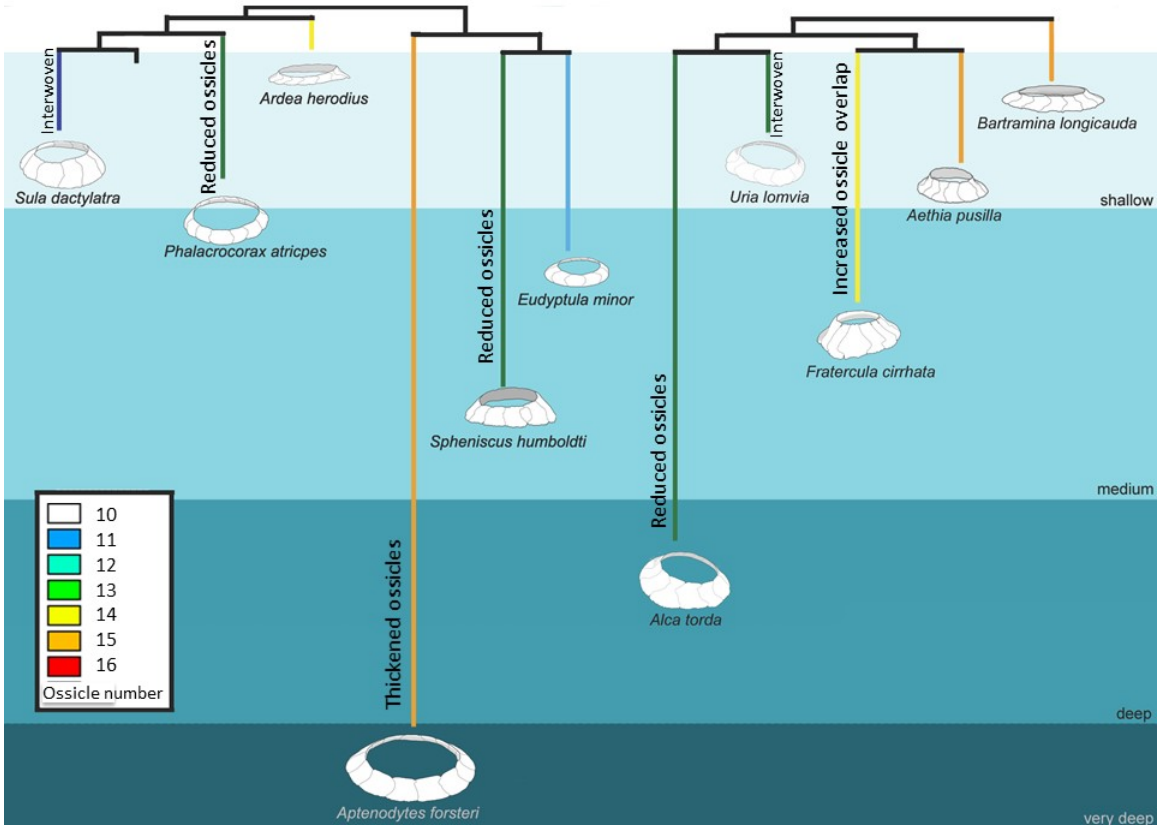
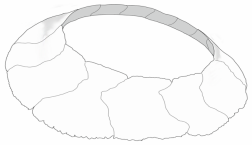
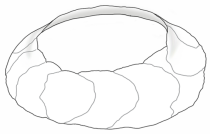


Figure 15. Changes in ossicle character by dive depth

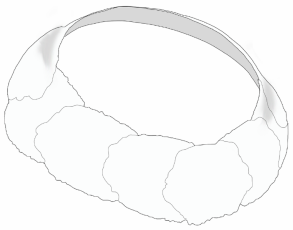
Changes in ossicle characteristics such as the presence of reduced ossicles, increased ossicle overlap, and interlocking ossicles are often found in clades where birds are diving deeply or impacting the water at high speeds. These changes could reinforce the ring making it better able to protect the eye from deformation.



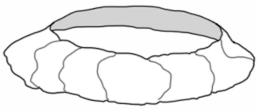
Alca torda
USNM 502379



Alle alle
AMNH 28452

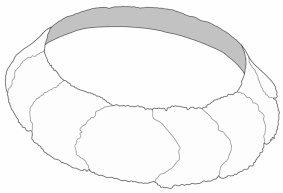


Uria lomvia
USNM 502367

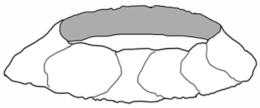


Brachyramphus brevirostris
UWBM 40384

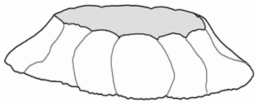
Cepphus columba
USNM 612988



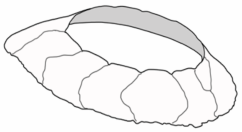
Uria aalge
USNM 502360



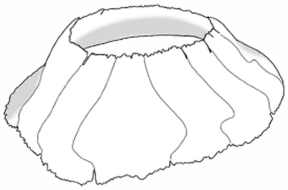
Synthliboramphus antiquus
UWBM 18433



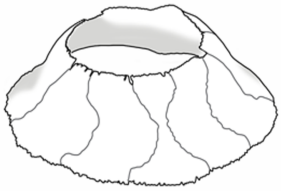
Synthliboramphus hypoleucus
AMNH 27408



Synthliboramphus wumizusume
UWBM 5587



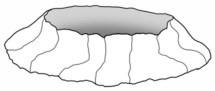
Fratercula cirrahata
USNM 556445



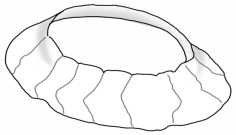
Fratercula corniculata
USNM 561939

Fratercula arctica
USNM 623288

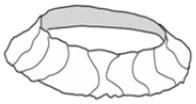
Aethia pusilla
UWBM 26627



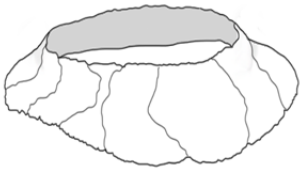
Aethia pygmaea
AMNH 21300



Aethia christatella
AMNH 21273



Xema sabini
UWBM 41088

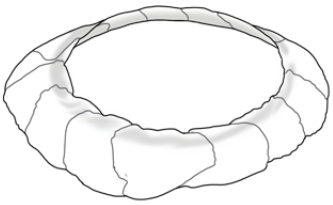


Rissa tridactyla
UWBM 31905

Larus marinus
AMNH 21913

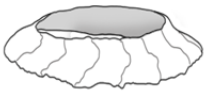
Sterna anaethetus
USNM 554972

Sterna maxima
UWBM 45817



Larus argentatus
AMNH 16370

Rhynchops niger
UWBM 36020

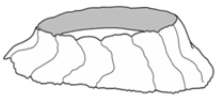


Bartramia longicauda
USNM 641407

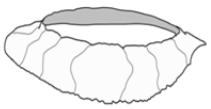
Anous tenuirostris
UWBM 18604

Charadrius wilsonia
AMNH 10653

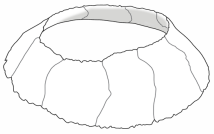
Numenius phaeopus
AMNH 26200



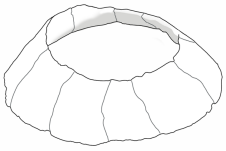
Gygis alba
UWBM 42617



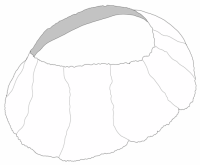
Charadrius vociferus
UWBM 62155



Sula dactylatra
USNM 498030

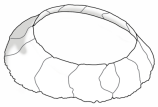


Sula bassana
AMNH 18805



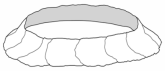
Morus capensis
USNM 558363

Phalacrocorax atriceps
USNM 489476

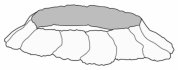


Phalacrocorax melanoleucos
USNM 561522

Phalacrocorax auritus
USNM 560554



Phalacrocorax carbo
UWBM 61351



Fregata ariel
USNM 498345

Ardea alba
UWBM 45809

Cochlearius cochlearius
USNM 613750

Eudocimus ruber
USNM 559150

Ardea herodias
UWBM 18618

Puffinus gravis
AMNH 17848

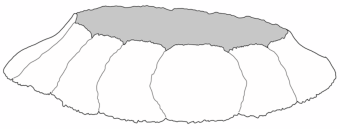
Fulmarus glacialis
AMNH 19556

Scopus umbretta
USNM 431669

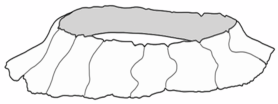
Puffinus gresius
AMNH 23453

Pterodroma neglecta
AMNH 23504

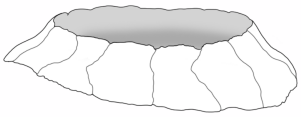
Pterodroma inexpectata
UWBM 55612



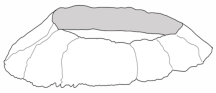
Thalassarche melanophris
UWBM 81016



Diomedea exulans
UWBM 81036

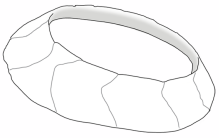


Phoebastria immutabilis
UWBM 39578

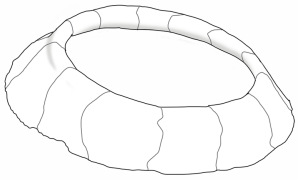


Spheniscus humboldti
UWBM 36133

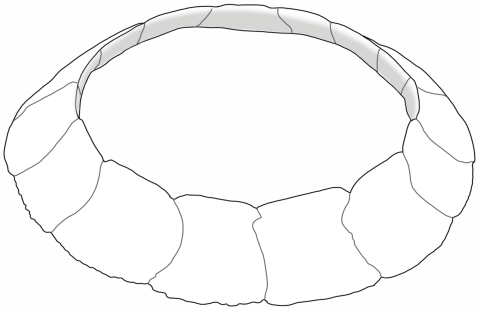
Spheniscus magellanicus
UWBM 57109



Pygoscelis adeliae
AMNH 26163



Eudyptes chrysolophus
USNM 491413



Aptenodytes forsteri
USNM 553580

Eudyptula minor
AMNH 29318

Illustration A. Scleral rings from a selection of waterbirds and Charadriiforms
Scale bar indicates 5mm

Appendices

APPENDIX A: MEASUREMENTS OF INDIVIDUAL SPECIMENS

Cat. Number	*Scientific name*	INT	EXT	SRH	OL
NMNH 502381	*Alca torda*	9.87	16.66	3.05	22.42
NMNH 502376	*Alca torda*	10.41	16.74	3.66	23.40
NMNH 501669	*Alca torda*	9.78	15.87	3.15	20.74
NMNH 502379	*Alca torda*	9.95	16.19	3.34	22.12
NMNH 555668	*Alca torda*	-	-	-	21.72
UNNM 491731	*Alca torda*	-	-	-	20.98
NMNH 502377	*Alca torda*	10.03	16.56	3.36	22.69
NMNH 502378	*Alca torda*	9.95	15.78	2.70	22.52
NMNH 502382	*Alca torda*	10.03	16.42	3.33	22.74
NMNH 18060	*Alca torda*	-	-	-	21.64
NMNH 501644	*Alca torda*	9.57	16.35	2.96	22.46
NMNH 555666	*Alca torda*	-	-	-	22.86
USNM 623285	*Alca torda*	10.53	16.23	3.04	21.19
USNM 623286	*Alca torda*	-	16.46	3.33	21.19
NMNH 502385	*Alca torda*	10.01	15.95	3.03	23.10
NMNH 502390	*Alca torda*	10.03	15.97	2.86	20.91
NMNH 502388	*Alca torda*	9.97	16.32	3.14	22.21
NMNH 502389	*Alca torda*	10.05	16.35	3.26	22.85
NMNH 502380	*Alca torda*	10.00	16.03	3.05	22.17
NMNH 502384	*Alca torda*	10.06	16.46	3.11	22.31
NMNH 502383	*Alca torda*	10.17	15.98	3.06	21.56
NMNH 502387	*Alca torda*	10.11	16.28	2.80	21.17
USNM 561915	*Uria lomvia*	11.64	16.72	3.09	23.61
USNM 500187	*Uria lomvia*	-	-	3.28	22.82
NMNH 499994	*Uria lomvia*	11.95	17.07	2.77	23.39
NMNH 502363	*Uria lomvia*	11.70	16.57	2.83	23.66
NMNH 500014	*Uria lomvia*	12.06	16.95	3.28	23.03
NMNH 500006	*Uria lomvia*	12.12	17.89	3.27	24.29
NMNH 502362	*Uria lomvia*	11.77	16.79	3.22	23.11
NMNH 502364	*Uria lomvia*	11.34	16.74	3.36	23.01
NMNH 502361	*Uria lomvia*	11.47	16.43	3.09	23.04
USNM 502367	*Uria lomvia*	11.63	16.30	2.76	23.16
NMNH 49936	*Uria lomvia*	11.90	17.60	3.39	23.06
USNM 623295	*Uria aalge*	11.20	15.24	2.91	22.61
USNM 623293	*Uria aalge*	11.18	16.48	3.32	22.75
USNM 623292	*Uria aalge*	11.75	16.62	2.84	22.99
USNM 621262	*Uria aalge*	11.31	16.81	3.19	23.15
USNM 623294	*Uria aalge*	11.27	16.25	3.05	22.49
NMNH 502360	*Uria aalge*	11.45	16.91	3.31	23.27

NMNH 502349	*Uria aalge*	11.81	16.76	3.09	23.38
NMNH 502352	*Uria aalge*	11.53	16.67	3.06	22.01
NMNH 502341	*Uria aalge*	11.53	16.67	3.24	22.54
NMNH 502342	*Uria aalge*	11.28	16.27	3.07	23.71
USNM 623290	*Cepphus grylle*	-	12.14	1.48	18.61
USNM 612213	*Cepphus grylle*	8.91	13.20	2.11	18.75
AMNH 17538	*Cepphus grylle*	7.93	12.39	1.58	17.95
AMNH17539	*Cepphus grylle*	8.22	12.16	1.71	18.03
AMNH 27881	*Cepphus grylle*	8.07	12.09	1.67	17.86
USNM 623291	*Cepphus grylle*	7.99	11.63	1.60	18.05
NMNH 498422	*Cepphus columba*	8.80	13.09	2.12	19.83
USNM 612988	*Cepphus columba*	8.71	12.76	2.32	19.59
NMNH 498420	*Cepphus columba*	8.58	13.09	1.79	19.70
NMNH 498424	*Cepphus columba*	8.65	13.65	2.10	19.98
NMNH 557623	*Cepphus columba*	8.41	12.85	1.83	18.67
USNM 612989	*Cepphus columba*	8.69	13.22	2.21	19.56
USNM 498421	*Cepphus columba*	-	-	-	19.90
NMNH 498423	*Cepphus columba*	9.03	13.47	2.29	19.35
NMNH 599498	*Brachyramphus marmoratus*	8.91	12.89	2.47	16.43
NMNH 557610	*Brachyramphus marmoratus*	8.56	12.83	2.23	18.33
NMNH 557620	*Brachyramphus marmoratus*	8.46	12.66	2.12	18.19
NMNH 557622	*Brachyramphus marmoratus*	8.66	12.78	2.32	17.65
NMNH 557616	*Brachyramphus marmoratus*	8.63	12.42	2.07	17.41
NMNH 557621	*Brachyramphus marmoratus*	8.90	12.94	2.19	18.44
NMNH 557617	*Brachyramphus marmoratus*	8.41	12.33	2.30	17.37
USNM 612990	*Brachyramphus marmoratus*	8.62	12.61	2.28	17.32
AMNH 29621	*Alle alle*	7.13	10.73	1.98	14.98
AMNH 28452	*Alle alle*	7.29	11.21	1.97	15.57
AMNH 28453	*Alle alle*	7.50	11.66	2.18	15.21
AMNH 24534	*Alle alle*	7.08	10.61	1.89	13.91
USNM 621558	*Aethia psittacula*	5.73	10.00	0.83	15.26
USNM 561928	*Aethia psittacula*	6.51	11.28	2.20	15.74
NMNH 557607	*Aethia psittacula*	5.78	10.18	1.72	14.14
USNM 561059	*Aethia psittacula*	7.14	11.07	2.27	14.92
NMNH 557609	*Aethia psittacula*	5.92	10.07	2.08	14.36
NMNH 557610	*Aethia psittacula*	6.81	11.11	2.18	14.35
NMNH 557608	*Aethia psittacula*	6.02	10.51	2.19	14.27
USNM 491845	*Aethia psittacula*	7.11	11.49	2.28	15.52
AMNH 21290	*Aethia cristatella*	7.17	10.97	1.72	15.32
AMNH 21275	*Aethia cristatella*	7.12	10.82	1.80	14.72
AMNH 21280	*Aethia cristatella*	7.21	11.11	2.05	14.80
AMNH 21296	*Aethia cristatella*	7.25	11.24	1.78	15.73
AMNH 21273	*Aethia cristatella*	7.47	11.53	2.18	15.86
AMNH 21272	*Aethia cristatella*	7.04	11.05	1.95	15.11
AMNH 21266	*Aethia cristatella*	7.06	11.01	1.95	14.64
AMNH 21289	*Aethia cristatella*	6.92	11.40	1.77	15.13

AMNH 21270	*Aethia cristatella*	6.93	11.00	1.91	15.01
NMNH 292344	*Fratercula arctica*	7.48	15.64	5.06	22.47
USNM 623288	*Fratercula arctica*	6.91	14.74	3.69	21.26
USNM 623289	*Fratercula arctica*	6.87	14.67	4.67	21.52
AMNH 16721	*Fratercula arctica*	6.85	14.86	3.82	22.26
AMNH 16724	*Fratercula arctica*	6.62	14.30	3.84	21.29
AMNH 16723	*Fratercula arctica*	6.50	14.10	3.91	22.69
AMNH 16730	*Fratercula arctica*	7.02	14.62	3.50	21.91
AMNH 16727	*Fratercula arctica*	6.70	15.29	3.89	22.95
USNM 499959	*Fratercula corniculata*	6.83	15.37	4.80	22.83
USNM 561938	*Fratercula corniculata*	7.35	15.16	4.64	22.55
USNM 561937	*Fratercula corniculata*	7.10	14.83	4.02	22.43
USNM 561940	*Fratercula corniculata*	7.43	15.04	4.01	21.33
NMNH 499964	*Fratercula corniculata*	7.70	15.09	4.27	23.69
USNM 561939	*Fratercula corniculata*	7.13	14.50	3.79	22.86
NMNH 556445	*Fratercula cirrhata*	8.56	15.64	3.52	23.56
NMNH 556448	*Fratercula cirrhata*	8.45	16.22	3.91	22.66
NMNH 556454	*Fratercula cirrhata*	8.43	16.51	4.92	23.14
USNM 561944	*Fratercula cirrhata*	8.08	16.23	3.74	24.32
USNM 561946	*Fratercula cirrhata*	8.00	16.12	4.05	23.15
USNM 561959	*Fratercula cirrhata*	7.31	15.63	4.07	23.34
USNM 561942	*Fratercula cirrhata*	7.86	16.02	4.40	23.91
NMNH 558358	*Fratercula cirrhata*	8.07	16.46	4.75	22.47
NMNH 556449	*Fratercula cirrhata*	7.23	15.78	4.32	22.03
USNM 553580	*Aptenodytes forsteri*	23.10	35.32	4.93	54.00
USNM 555520	*Aptenodytes forsteri*	23.50	34.05	3.92	53.91
AMNH 29794	*Aptenodytes forsteri*	23.51	33.99	3.99	49.28
AMNH 8111	*Aptenodytes forsteri*	22.30	32.73	4.08	48.68
AMNH 11634	*Aptenodytes forsteri*	23.77	34.06	4.89	52.95
AMNH 8112	*Aptenodytes forsteri*	22.41	32.92	4.35	51.33
AMNH 3600	*Aptenodytes forsteri*	19.53	34.13	4.27	55.00
USNM 491413	*Eudyptes chrysolophus*	15.82	24.21	4.55	32.91
AMNH 27337	*Eudyptes chrsocome*	13.75	20.84	3.81	28.50
AMNH 27336	*Eudyptes chrsocome*	14.75	22.04	4.71	28.73
AMNH 26509	*Eudyptes pachyrynchus*	17.31	25.07	5.72	34.17
USNM 014493	*Phalacrocorax verrucosus*	-	-	-	21.02
USNM 612655	*Phalacrocorax varius*	9.73	13.95	2.76	17.74
USNM 490792	*Phalacrocorax atriceps*	10.90	15.53	3.24	21.07
USNM 489476	*Phalacrocorax atriceps*	12.85	17.21	2.68	22.19
USNM 490851	*Phalacrocorax atriceps*	10.94	15.31	1.98	21.37
USNM 489486	*Phalacrocorax atriceps*	12.23	15.91	2.54	22.02
AMNH 26168	*Phalacrocorax atriceps*	11.99	16.78	2.90	23.59
USNM 561525	*Phalacrocorax malanoleucus*	8.20	12.23	2.05	14.05
USNM 561530	*Phalacrocorax malanoleucus*	5.82	10.15	1.54	15.95
USNM 561523	*Phalacrocorax malanoleucus*	8.11	11.77	2.07	-
USNM 561522	*Phalacrocorax malanoleucus*	8.61	12.57	2.52	14.73

USNM 561527	*Phalacrocorax malanoleucus*	-	11.79	2.16	13.60
USNM 561533	*Phalacrocorax malanoleucus*	7.37	11.77	2.11	15.68
AMNH 23561	*Phalacrocorax magellanicus*	8.78	12.26	1.87	19.06
AMNH 23558	*Phalacrocorax magellanicus*	9.56	12.97	1.68	19.09
AMNH 23571	*Phalacrocorax magellanicus*	9.86	12.91	2.24	19.02
AMNH 23559	*Phalacrocorax magellanicus*	8.76	13.73	1.72	19.19
AMNH 23560	*Phalacrocorax magellanicus*	9.59	12.54	1.90	18.80
AMNH 23581	*Phalacrocorax magellanicus*	8.93	12.64	2.33	17.47
NMNH 502337	*Sula Bassanus*	13.56	21.39	3.69	30.49
NMNH 502180	*Sula Bassanus*	12.93	20.88	4.81	29.40
AMNH 2926	*Sula Bassanus*	13.20	21.63	5.11	29.82
AMNH 20909	*Sula Bassanus*	13.36	21.31	5.21	30.35
AMNH 18805	*Sula Bassanus*	13.42	21.19	5.22	31.00
AMNH 15920	*Sula Bassanus*	12.98	21.89	5.10	30.33
USNM 498133	*Sula dactylatra*	12.86	20.93	5.53	28.13
USNM 498028	*Sula dactylatra*	11.54	20.61	4.93	26.84
USNM 498030	*Sula dactylatra*	10.94	19.69	5.05	25.88
USNM 498370	*Sula dactylatra*	11.81	19.95	5.92	24.64
AMNH 1452	*Sula dactylatra*	11.68	21.20	6.43	26.32
AMNH 1372	*Sula dactylatra*	11.11	19.41	5.45	25.22
AMNH 2988	*Sula dactylatra*	11.38	20.57	4.71	24.39
NMNH 558368	*Sula capensis*	11.91	18.97	4.13	29.16
NMNH 558369	*Sula capensis*	11.97	19.44	3.78	29.01
NMNH 558370	*Sula capensis*	11.93	19.47	4.13	28.94
NMNH 558367	*Sula capensis*	11.61	19.66	4.74	28.17
AMNH 1235	*Sula capensis*	12.22	18.81	4.99	28.73
NMNH 490902	*Pelecanoides urinatrix*	6.04	9.46	1.63	13.81
USNM 490896	*Pelecanoides urinatrix*	5.69	9.33	1.33	12.96
USNM 490896	*Pelecanoides urinatrix*	5.49	9.46	1.63	13.04
NMNH 553242	*Pelecanoides urinatrix*	6.45	9.73	1.72	14.78
AMNH 27320	*Pelecanoides urinatrix*	6.52	9.55	1.27	13.87
AMNH 23454	*Pelecanoides garnotii*	7.07	11.17	1.74	16.14
AMNH 23458	*Pelecanoides garnotii*	6.72	11.00	1.52	15.43
AMNH 23452	*Pelecanoides garnotii*	5.91	9.84	1.25	15.04
AMNH 23450	*Pelecanoides garnotii*	6.98	10.81	1.55	15.49
AMNH 23457	*Pelecanoides garnotii*	6.84	10.66	1.90	15.46
AMNH 23456	*Pelecanoides garnotii*	7.19	11.10	1.55	15.86
USNM 621490	*Pelecanus occidentalis*	15.37	21.32	4.12	40.64
USNM 621489	*Pelecanus occidentalis*	14.71	21.74	3.23	40.33
AMNH 3618	*Pelecanus occidentalis*	13.53	19.60	2.68	39.53
AMNH 21610	*Pelecanus occidentalis*	13.51	19.46	3.22	37.19
AMNH 26310	*Gavia immer*	15.09	23.73	4.59	30.99
AMNH 11033	*Gavia immer*	14.73	22.49	4.65	29.62
AMNH 10778	*Gavia immer*	15.57	23.46	4.20	29.73
AMNH 16690	*Gavia immer*	15.18	22.15	3.58	29.75
AMNH 15919	*Gavia immer*	15.80	24.12	4.58	29.97

AMNH 23587	*Gavia immer*	16.00	24.34	4.39	29.96
AMNH 23594	*Gavia immer*	14.84	23.61	4.82	30.86
AMNH 23097	*Gavia immer*	15.64	23.02	4.26	30.54
AMNH 23106	*Gavia immer*	15.08	24.09	5.18	31.20
AMNH 23100	*Gavia immer*	15.13	23.02	3.88	31.63
AMNH 2351	*Fregata magnificens*	11.23	17.95	3.20	28.29
AMNH 21469	*Fregata magnificens*	12.41	17.71	3.34	26.18
AMNH 23506	*Diomedea melanophris*	12.87	20.88	3.62	36.39
AMNH 3135	*Diomedea melanophris*	13.41	20.35	4.36	36.60
AMNH 1438	*Diomedea cauta*	14.90	21.51	3.89	36.85
AMNH 1441	*Diomedea cauta*	14.28	21.93	3.34	35.65
AMNH 24565	*Larus argentatus*	10.75	16.74	2.64	25.68
AMNH 26049	*Larus argentatus*	10.57	15.86	2.00	28.81
AMNH 16370	*Larus argentatus*	10.67	15.76	1.81	23.73
AMNH 18308	*Larus argentatus*	11.17	17.46	2.65	25.97
AMNH 24569	*Larus argentatus*	10.86	16.85	2.09	25.82
AMNH 10377	*Larus argentatus*	11.05	16.82	2.09	24.77
AMNH 21913	*Larus marinus*	11.84	18.15	3.90	28.73
AMNH 21914	*Larus marinus*	11.71	18.35	3.90	28.27
AMNH 24571	*Larus marinus*	11.78	17.41	2.52	27.44
AMNH 24578	*Larus marinus*	11.43	16.94	2.25	26.49
AMNH 23544	*Puffinus griseus*	8.60	12.56	1.31	17.97
AMNH 16720	*Puffinus griseus*	8.49	12.42	1.45	18.09
AMNH 23545	*Puffinus griseus*	8.29	12.58	1.32	18.09
AMNH 23543	*Puffinus griseus*	8.44	12.00	1.26	17.24
AMNH 27178	*Puffinus gravis*	9.95	13.76	1.91	19.46
AMNH 16717	*Puffinus gravis*	9.22	13.07	1.48	18.58
AMNH 17484	*Puffinus gravis*	9.54	14.05	2.23	19.97
AMNH 29318	*Eudyptula minor*	11.60	18.04	3.48	24.21
AMNH 27317	*Eudyptula minor*	10.72	16.55	3.01	23.12
AMNH 26164	*Pygoscelis adeliae*	15.15	23.08	3.31	33.75
AMNH 26163	*Pygoscelis adeliae*	16.08	23.21	3.92	31.76
AMNH 26162	*Pygoscelis adeliae*	14.74	21.37	3.99	32.48
AMNH 21834	*Pygoscelis adeliae*	14.58	22.30	3.73	33.58
UWBM 48018	*Brachyramphus brevirosrtis*	8.52	12.48	2.13	17.09
UWBM 43084	*Brachyramphus brevirosrtis*	8.24	12.19	2.50	17.61
UWBM 18433	*Synthliboramphus antiquus*	8.16	10.84	2.07	16.40
UWBM 39594	*Synthliboramphus antiquus*	6.28	15.66	1.88	15.51
UWBM 55695	*Synthliboramphus wumizusume*	6.94	10.28	1.87	16.78
UWBM 55587	*Synthliboramphus wumizusume*	6.73	10.70	1.88	16.68
UWBM 54879	*Synthliboramphus hypoleucus*	7.41	12.42	2.49	18.24
AMNH 27408	*Synthliboramphus hypoleucus*	7.57	11.88	2.12	17.57
AMNH 21304	*Aethia pygmaea*	6.80	10.63	1.86	14.55
AMNH 21300	*Aethia pygmaea*	6.46	10.31	1.79	13.98

AMNH 20722	*Ptychoramphus aleuticus*	6.76	11.21	1.73	15.31
AMNH 20709	*Ptychoramphus aleuticus*	6.71	11.20	1.74	15.17
UWBM 26627	*Ptychoramphus pusilla*	6.19	9.85	1.83	13.27
UWBM 30098	*Ptychoramphus pusilla*	5.77	8.86	1.49	13.19
USNM 557613	*Cerorhinca monocerata*	7.42	15.10	3.44	21.28
USNM 620643	*Cerorhinca monocerata*	7.11	14.62	3.17	21.30
USNM 557614	*Cerorhinca monocerata*	7.97	14.83	3.12	20.80
UWBM 44123	*Stericoraridae longicaudus*	8.08	12.24	2.16	19.14
UWBM 48495	*Stericoraridae longicaudus*	8.51	13.68	2.08	19.68
AMNH 23474	*Larosterna inca*	6.94	11.63	1.61	18.95
AMNH 23477	*Larosterna inca*	7.20	11.56	1.50	18.33
UWBM 38264	*Sterna maxima*	9.05	14.89	3.47	27.04
UWBM 45817	*Sterna maxima*	9.19	15.15	3.74	27.98
USNM 488397	*Sterna anaethetus*	7.36	11.27	2.42	18.24
USNM 554972	*Sterna anaethetus*	8.13	12.05	2.61	21.38
UWBM 42593	*Gygris alba*	7.93	12.54	2.50	19.18
UWBM 42617	*Gygris alba*	7.96	12.24	2.00	19.76
UWBM 36020	*Ryncops niger*	8.36	11.93	1.00	17.96
UWBM 45695	*Ryncops niger*	-	-	1.32	17.17
UWBM 41088	*Xema sabini*	6.99	10.41	1.17	16.56
UWBM 41087	*Xema sabini*	6.95	10.63	1.54	16.23
UWBM 31904	*Rissa tridactyla*	10.03	14.86	1.90	23.36
UWBM 31905	*Rissa tridactyla*	9.89	15.03	2.28	22.38
USNM 491607	*Rhodostethia rosea*	8.36	12.18	2.22	17.78
USNM 491609	*Rhodostethia rosea*	8.71	12.49	1.85	19.29
UWBM 18604	*Anous tenuirostris*	6.04	9.50	0.97	15.85
USNM 641347	*Glareola pratincola*	7.78	11.04	1.41	16.46
USNM 429182	*Cursorius temminckii*	6.18	10.74	2.41	13.68
USNM 641407	*Bartramia longicauda*	6.95	10.23	1.25	14.68
USNM 641412	*Bartramia longicauda*	6.06	9.68	1.08	15.31
AMNH 26200	*Numenius phaeopus*	8.56	12.77	1.45	18.96
AMNH 27991	*Numenius phaeopus*	8.05	12.50	1.31	18.81
UWBM 62155	*Charadrius vociferus*	7.70	11.25	1.26	14.91
UWBM 88818	*Charadrius vociferus*	7.49	10.73	1.04	14.44
AMNH 10224	*Charadrius wilsonia*	7.15	10.03	1.09	13.73
AMNH 10653	*Charadrius wilsonia*	7.03	10.19	1.33	13.91
UWBM 33446	*Pluvianus aegyptius*	6.33	9.55	1.09	13.01
UWBM 55189	*Scolopax minor*	9.10	13.06	1.23	14.89
UWBM 57803	*Scolopax minor*	8.97	12.76	1.04	15.39
UWBM 57109	*Spheniscus magellanicus*	14.96	21.75	3.58	25.51
UWBM 57103	*Spheniscus magellanicus*	15.20	23.02	3.03	28.40
UWBM 39907	*Spheniscus humboldti*	12.70	19.04	3.27	28.80
UWBM 36133	*Spheniscus humboldti*	12.60	19.34	3.23	28.32
UWBM 79017	*Spheniscus humboldti*	12.79	20.16	3.51	26.95
UWBM 19856	*Spheniscus humboldti*	14.56	21.66	4.01	27.98
AMNH 12616	*Spheniscus humboldti*	13.36	20.23	3.62	29.89

USNM630846	*Spheniscus demersus*	14.39	21.63	4.25	29.08
AMNH1625	*Spheniscus demersus*	13.18	20.94	4.56	30.55
AMNH26471	*Aptenodytes patagonica*	20.94	29.67	4.88	44.84
AMNH1623	*Aptenodytes patagonica*	19.17	28.30	5.13	44.32
AMNH 26472	*Aptenodytes patagonica*	22.30	31.43	4.93	44.99
USNM 560554	*Phalacrocorax auritus*	10.27	13.80	1.92	17.47
USNM 560562	*Phalacrocorax auritus*	10.53	14.95	1.89	18.42
UWBM 81036	*Diomedia exulans antipodensis*	15.91	23.54	3.61	36.94
UWBM 81037	*Diomedia exulans gibsoni*	15.88	23.84	2.60	41.62
UWBM 38292	*Nyctanassa violacea*	13.91	19.54	2.04	27.40
UWBM 45809	*Ardea alba*	10.13	14.91	2.34	17.02
UWBM 79472	*Ardea alba*	10.45	15.07	2.03	16.86
UWBM 19947	*Ardea herodius*	15.13	21.48	2.85	23.86
UWBM 18618	*Ardea herodius*	14.62	19.80	2.94	25.57
UWBM 47044	*Ixobrynchus eurhythmus*	6.99	10.23	1.13	10.39
UWBM 47059	*Ixobrynchus eurhythmus*	7.18	10.17	1.05	10.46
UWBM 55612	*Pterodroma inexpectata*	9.95	14.91	1.86	19.63
UWBM 55694	*Pterodroma inexpectata*	9.69	14.35	1.75	19.78
UWBM 81004	*Thalassarche cauta steadi*	15.91	24.00	3.56	34.32
UWBM 81016	*Thalassarche cauta steadi*	15.69	23.87	4.20	32.42
UWBM 50634	*Gavia pacifica*	11.85	17.91	3.20	23.51
UWBM 50641	*Gavia pacifica*	11.38	17.42	3.35	22.40
UWBM 14217	*Aechmophorus occidentalis*	8.51	12.72	2.53	16.49
UWBM 14181	*Aechmophorus occidentalis*	9.09	12.97	2.57	15.67
UWBM 47782	*Gavia stellata*	10.15	15.86	2.91	21.47
UWBM 38284	*Gavia stellata*	10.42	15.50	2.34	20.56
UWBM 43235	*Phoebastria immutabilis*	13.71	20.37	3.06	32.38
UWBM 39578	*Phoebastria immutabilis*	14.01	20.50	4.10	30.52
UWBM 55329	*Puffinus carneipes*	9.22	13.28	1.62	18.86
UWBM 55319	*Puffinus carneipes*	8.76	13.01	1.58	19.32
AMNH 20699	*Fulmaris glacialis*	9.87	13.99	1.58	19.82
AMNH 19556	*Fulmaris glacialis*	9.61	13.65	1.50	18.94
AMNH 23494	*Pterodroma externa*	8.93	13.94	2.43	19.50
AMNH 23496	*Pterodroma externa*	8.97	14.28	2.43	19.77
AMNH 23505	*Pterodroma neglecta*	9.56	13.99	1.81	19.66
AMNH 23504	*Pterodroma neglecta*	9.64	14.06	2.09	19.92
AMNH 18492	*Oceanodroma furcata*	5.88	8.22	0.71	11.28
AMNH 22041	*Oceanodroma furcata*	5.72	8.42	0.82	10.87
USNM 614821	*Oceanities oceanicus*	4.76	6.58	0.51	9.86
USNM 488308	*Oceanities oceanicus*	4.72	6.61	0.48	9.70
USNM 613734	*Cochlearius cochlearius*	15.45	20.27	2.33	28.23
USNM 612256	*Cochlearius cochlearius*	17.42	23.76	2.41	31.37
USNM 559150	*Eudocimus ruber*	8.67	13.49	1.59	18.60
USNM 558254	*Eudocimus ruber*	9.05	12.93	1.25	20.43
USNM 497971	*Fregata ariel*	10.12	15.84	2.64	22.03
USNM 498345	*Fregata ariel*	10.80	16.31	2.55	23.73

USNM 623232	*scopus umbretta*	10.00	14.24	0.73	20.23
USNM 431669	*scopus umbretta*	10.28	14.26	0.61	20.75
UWBM 61351	*Phalacrocorax carbo*	10.57	14.93	1.75	19.14
UWBM 62870	*Phalacrocorax carbo*	9.88	13.84	2.08	18.65
UWBM 51934	*Bucephala islandica*	9.45	14.69	1.68	21.79
USNM 488597	*Bucephala islandica*	8.40	12.84	1.38	18.51
UWBM 18424	*Bucephala albeola*	6.81	11.41	1.34	16.63
UWBM 20615	*Bucephala albeola*	8.02	11.71	1.72	16.81
UWBM 40038	*Merganser serrator*	8.82	12.90	1.52	18.73
UWBM 59587	*Merganser serrator*	8.79	12.68	1.63	18.37
UWBM 59228	*Pelecanus erythrorhychos*	13.35	19.70	1.65	33.98
UWBM 59302	*Pelecanus erythrorhychos*	13.64	21.00	2.22	36.61
USNM 558366	*Pelecanus onocrotalus*	14.30	20.33	1.82	34.02
USNM 555612	*Pelecanus onocrotalus*	15.66	20.87	1.97	35.67
USNM 491300	*Larus occidentalis*	10.05	15.04	1.53	23.13
USNM 491277	*Larus occidentalis*	10.52	16.19	1.58	25.55

APPENDIX B: ACTIVITY PATTERN

Taxon	**Activity Pattern**	**Source**
Charadriiformes		
Alle alle	cathemeral	Bradstreet & Brown 1985
Uria lomiva	diurnal	Falk et al. 2002
Uria aalge	diurnal	Camphuysen 1998
Cepphus grylle	cathemeral	McNeil et al. 1993
Cepphus columba	diurnal	McNeil et al. 1993
Brachyramphus marmoratus	diurnal	McNeil et al. 1993
Synthliboramphus antiquus	diurnal	McNeil et al. 1993
Aethia pygmaea	diurnal	Byrd et al. 1983
Aethia aleuticus	nocturnal	Watanuki 1986
Aethia cristatella	diurnal	Byrd et a.l 1983
Aethia psittacula	diurnal	Hatch 2002
Aethia pusilla	diurnal	Bedard 1969
Cerrorhinca monocerata	cathemeral	Watanuki 1990
Fratercula corniculata	diurnal	Hatch 2002
Fratercula arctica	diurnal	McNeil et al. 1993
Fratercula cirrhata	diurnal	McNeil et al. 1993
Alca torda	diurnal	Antonia et al. 2001
Larus argentatus	cathemeral	McNeil et al. 1993
Larus occidentalis	cathemeral	McNeil et al. 1993
Larus marinus	cathemeral	McNeil et al. 1993
Rissa tridactyla	cathemeral	McNeil et al. 1993
Sterna maxima	diurnal	Erwin 1977
Sterna anaethetus	cathemeral	Dunlop 1997
Ryncops niger	diurnal	Erwin 1977

Ixobrychus eurhythmus	nocturnal	McNeil et al. 1993
Egretta alba	cathemeral	McNeil et al. 1993
Ardea herodias	cathemeral	McNeil et al. 1993
Nycticorax violaceus	nocturnal	McNeil et al. 1993

Water Birds (Clade H)

Sula dactylatra	diurnal	Weimerskirch et al. 2008
Morus bassanus	diurnal	Garth et al., 2003
Phalacrocorax varius	diurnal	McNeil et al. 1993
Phalacrocorax auritus	diurnal	Hatch et al. 1999
Phalacrocorax carbo	diurnal	King et al. 1998
Fulmarus glacialis	nocturnal	McNeil et al. 1993
Pterodroma externa	diurnal	McNeil et al. 1993
Pterodroma inexpectata	cathemeral	McNeil et al. 1993
Puffinus puffinus	cathemeral	Watanuki 1986
Puffinus carneips	diurnal/cathemeral	McNeil et al. 1993
Puffinus gravis	nocturnal	McNeil et al. 1993
Puffinus griseus	cathemeral	McNeil et al. 1993
Oceanites oceanicus	cathemeral	McNeil et al. 1993
Oceanodroma furcata	nocturnal	McNeil et al. 1993
Pelecanoides garnoti	cathemeral	McNeil et al. 1993
Pelecanoides urinatrix	cathemeral	McNeil et al. 1993
Diomedeidae exulans	cathemeral	McNeil et al. 1993
Thalassarche cauta	diurnal	Hedd et al. 2001
Thalassarche melanophris	cathemeral	Weimerskirch & Guionnet 2002
Phobastria immutabilis	nocturnal	McNeil et al. 1993
Aptenodytes forsteri	cathemeral	McNeil et al. 1993
Aptenodytes patagonicus	cathemeral	Moore et al. 1999
Spheniscus magellanicus	cathemeral	Scolaro & Suburo 1991
Eudyptula minor	cathemeral	Cannel & Cullen 2008
Eudyptes crysocome	diurnal	Tremblay & Cherel 2000
Eudyptes chrysolophus	diurnal	Green et al. 1998
Pygoscelis adeliae	diurnal	Wilson et al. 1989
Gavia immer	diurnal	Evers et al. 2010

APPENDIX C: MAXIMUM DIVE DEPTHS

Taxon	Common Name	Maximum Dive	Reference
Aptenodytes forsteri	emperor penguin	265	Kooyman et al. 1992
Aptenodytes patagonicus	king penguin	304	Kooyman et al. 1972

Eudyptes chrysocome	macaroni penguin	27	Croxall et al. 1993
Eudyptula minor	little blue penguin	27	Hull 2007
Pygoscelis adeliae	adelie Penguin	180	Watanuki et al. 1993
Pygoscelis antarctica	chinstrap penguin	70	Lishman and Croxall 1987
Spheniscus demersus	african Penguin	unknown	
Speniscus humboldti	humboldt penguin	53	Luna-Jorquera & Culik 1999
Spheniscus magellanicus	magellanic penguin	90	Scolaro & Suburo 1991
Gavia immer	common loon	70	Beletsky 2006
Diomedea exulan	wandering albatross	0.3	Prince et al. 1994
phoebastria immutabilis	laysan albatross	unknown	
Thalassarche cauta	shy albatross	7.4	Hedd et al. 1997
Thalassarche melanophris	black-browed albatross	4.5	Prince et al. 1994
Puffinus carneipes	flesh-footed shearwater	14.1	Taylor 2008
Puffinus gravis	great shearwater	5	Brown et al. 1981
Puffinus grieus	sooty shearwater	10	Brown et al. 1981
Fulmaris glacialis	northern fulmar	0.5	Wahl 1984
Pterodroma garnotii	peruvian diving petrel	85	Jahncke & Zavalaga 1997
Pelecanoides urinarix	common diving petrel	7.8	Taylor 2008
Oceanodroma furcata	fork-tailed storm petrel	unknown	
Pelecanus occidentalis	brown pelican	unknown	
Anhinga anhinga	american darter	unknown	
Anhinga melanogaster	african darter	5	Ryan 2007
Phalacrocorax atriceps	imperial shag	30	Quintana et al. 2007

Phalacrocorax varius	australian pied cormorant	unknown	
Phalacrocorax carbo	great cormornat	35	Grémillet et al. 1999
Phalacrocorax malenoleucus	little pied cormorant	unknown	
Morus bassanus	northern gannet	24	Ropert-courdert et al. 2009
Sula capensis	cape gannet	9	Adams & Walter 1993
Sula dactylatra	masket gannet	12	Nelson 1978
Alca torda	razorbill	120	Piatt & Nettleship 1985
Aethia cristatella	crestsed auklet	unknown	
Aethia psittacula	parakeet auklet	5	Gaston & Jones 1998
Aethia pusilla	least auklet	20	Gaston & Jones 1998
Aethia pygmaea	whisktered auket	unknown	
Alle alle	dovekie	unknown	
Bracyramphus marmoratus	marbled murrelet	80	Gaston & Jones 1998
Cepphus carbo	spectacled guiletmot	20	Gaston & Jones 1998
Cepphus columba	pigeon guilletmot	45	Ewins 1993
Cepphus grylle	black guilletmot	50	Gaston & Jones 1998
Cerorhinca monocerata	rhinocerous auklet	30	Burger et al. 1993
Fratercula arctica	atlanitc puffin	40	Spencer 2012
Fractercula cirrhata	tufted puffin	unknown	
Fratercula corniculata	horned puffin	unknown	
Ptychoramphus aleuticus	cassin's auklet	28	Burger & Powell 1990
Rissa tridactyla	black-legged kittiwake	0.04	Wahl 1984
Synthliboramphus hypoleucus	xantu's murrelet	20	Gaston & Jones 1998

Synthliboramphus antiquus	ancient murrelet	20	Gaston & Jones 1998
Synthliboramphus wumizusume	japanese murrelet	40	Gaston & Jones 1998

APPEDIX D: CHARACTERS SCORES

Taxon	INT serration	EXT serration	Overlap	Inter-woven	Scallop	Ossicle Number	Modal ossicle Number
Alca torda	0	1	1	2	1	2/3	3
Alle alle	0	1	1	0	0	3/4/5	3
Uria aalge	0	1	1	2	1	0/2/3/4	3
Uria lomvia	0	1	1	0	1	1/2/3/4	3
Cepphus columba	0	1	1	2	1	3/4	3
Cepphus grylle	0	0	1	0	1	2/3/4	3
Brachyramphus brevirostris	1	1	1/2	0	0	3	3
Brachyramphus marmoratus	1	1	2	0	0	3	3
Sythliboramphus antiqus	0	1	1	0	0	3	3
Synthliboramphus wumizusume	0	1	1/2	0	0	3	3
Synthliboramphus hypoleucus	0	1	1	0	1	1/2/3	1/2/3
Aethia crisatella	1	1	2	1	0	4/5/6	5
Aethia pygmae	0	1	1	0	0	5/6	5/6
Aethia psittacula	1	1	2	0	0	5/6	6
Aethia pusilla	1	1	1/2	0	0	2/4	5
Ptychoramphus aleuticus	0	1	2	0	1	4/5	4/5
Fratercula Arctica	2	2	2	0	1	4	4
Fratercula corniculata	2	2	2	0	1	3/4	4
Fratercula cirrhata	2	2	2	0	1	3/4	4
Cerorhinca monocerata	2	1	2	0	1	4	4
Stercorarius longicaudus	0	0	0/1	0	0	5	5
Larosterna inca	0	0	1	0	1	5	5
Sterna maxima	1	1	1	1	0	6	6
Sterna anaethetus	0	1	1	0	1	4	4
Gygis alba	0	0	1	1	0	5	5
Rynchops niger	0	1	1	0	0	5	5
Xema sabini	0	1	1	0	0	5	5
Rissa tridactyla	0	1	1/2	0	1	5	5
Larus argentatus	0	1	1/2	1	0	4/5/6	5
Larus marinus	0	1	1	0	0	5/6	5
Larus occidentalis	0	1	1	0	0	?	?
Rhodostethia rosea	0	0	1	0	?	4/5	5
Anous tenuirostris	0	0	0	0	0	3	3
Glareola pratincola	0	0	1	0	0	?	?

Cursorius temminckii	0	1	1	0	0	4	4
Scolopax minor	0	1	1/2	0	0	4/5/6	4/5/6
Bartramina longicauda	0	0	1	0	1	5	5
Numenius phaeopus	0	0	2	0	0	2/3/4	3
Charadrius vociferus	0	0	1	0	0	5	5
Charadrius wilsonia	0	0	2	0	0	4	4
Phalacrocorax varius	0	1	1	1	1	3	3
Phalacrocorax melanoleucos	0	0	1	1	0	1/2/3	2/3
Phalacrocorax atriceps	0	0	1	2	0/1	3	3
Phalacrocorax magellanicus	0	0	1	1	0	3/4/5	3
Phalacrocorax auritus	0	1	1	2	1	2/3	3
Phalacrocorax carbo	0	1	1	2	0	3/4	3/4
Anhinga melanogaster	0	1	1	0	0	2	2
Anhinga anhinga	0	1	1	1	1	2	2
Sula dactylatra	0	1	0/1	1	0	0/1	0
Morus bassanus	0	0	0	1	0	1/2/3	2
Morus capensis	1	1	0	0	0	2	2
Fregata magnificens	0	0	1	1	1	4/5/6	5
Fregata ariel	0	1	1	2	1	4/5	4/5
Ardea alba	0	1	2	0	0	4	4
Ardea herodius	1	1	1	0	1	4	4
Cochlearius cochlearius	0	1	1	0	1	4/5	4
Eudocimus ruber	0	1	1	0	1	5	5
Scopus umbretta	0	1	1	0	1	5	5
Pelecanus occidentalis	0	1	1	0	1	4/5/6	5
Pelecanus onocrotalus	0	1	1	0	1	6/7	7
Pelecanus erythrorhynchos	0	1	1	1	0	6/7	7
Thalassarche melanophris	0	0/1	1	0	0	5	5
Thalassarche cauta	0/1	1	1	0	0	5/6	5
Diomedia exulans	1	1	1	0	0	5/6	5
Phoebastria immutabilis	0	1	1	0	0	5/6	5/6
Oceanodroma furcata	0	1	1	0	1	3/4	3/4
Pelecanoides urinatrix	0	0	1	0	0	3/4	3
Pelecanoides garnotii	0	0	1	1	0	3/4/5	4
Puffinus carneipes	0	1	1	0	1	4/5	5
Puffinus gravis	0	1	1	0	1	5/6	5
Puffinus griseus	0	1	1	0	1	4/5/6	5
Pterodroma externa	0	0	1	1	0	3/4/5	4
Pterodroma neglecta	0	0	1	2	1	4	4
Pterodroma inexpectata	0	0	1	0	0	4/5	4/5
Oceanites oceanicus	0	1	1	0	1	4/5	4
Fulmaris glacialis	0	0	1	0	0	4/5	4/5
Eudyptula minor	0	0	1	0	0	1/2/3	1
Spheniscus magellanicus	0	1	1	0	0	3/4	3/4
Spheniscus humboldti	0	1	1	1	0	1/2/3	3

Spheniscus demersus	0	1	1	0	0	3	3
Pygoscelis adeliae	0	1	1	0	0	2/3	2
Aptenodytes forsteri	0	1	1	0	0	3/5/6	5
Aptenodytes patagonicus	0	1	1	1	0	4/5	5
Eudyptes chrysolophus	0	1	1	0	0	4	4
Eudyptes chrysocome	0	0	1	0	0/1	1/2/3/4	1/2/3/4
Eudyptes pachyrhynchus	0	1	1	0	0	2/3	2/3
Gavia immer	0	1	1	2	0	4/5/6	4
Gavia stellata	1	1	1	2	0	4	4
Gavia pacifica	0	1	1	0	1	2/4	2/4
Aechmophorus occidentalis	1	0	1	0	0	4/5	5
Corythaixoides concolor	0	0	1	0	0	3	3
Musophaga rossae	0	1	1	0	0	3	3

APPENDIX E: NUMBER OF RINGS EVALUATED PER SPECIES

Taxon	**Common name**	**No. of Specimens**	**No. of Rings**
Alca torda	Razorbill	21	36
Alle alle	Dovekie	4	8
Uria aalge	Common Murre	10	20
Uria lomvia	Thick-billed Murre	10	18
Cepphus columba	Pigeon Guillemot	8	16
Cepphus grylle	Black Guiillemot	6	11
Brachyramphus brevirostris	Kittlitz's Murrelet	2	4
Brachyramphus marmoratus	Marbled Murrelet	8	14
Sythilboramphus antiquis	Ancient Murrlelet	2	4
Sythilboramphus wumizusume	Japanese Murrelet	2	4
Sythilboramphus hypoleucus	Xantu's Murrelet	2	4
Fratercula artica	Atlantic Puffin	8	15
Fratercula corniculata	Horned Puffin	6	12
Fratercula cirrhata	Tufted Puffin	9	18
Cerrorhinca monocerata	Rhinocerous Auklet	3	6
Ptychoramphus aleuticus	Cassin's Auklet	2	4
Aethia cristatella	Crested Auklet	10	19
Aethia pygmae	Whiskered Auklet	2	4
Aethia pusilla	Least Auklet	2	4
Aethia psittacula	Parakeet Auklet	8	12
Stercorarius longicaudus	Long-tailed Skua	2	4
Xema sabini	Sabine's Gull	2	4
Rissa tridactyla	Black-legged Kittiwake	2	4
Larus argentatus	Herring Gull	6	12
Larus occidentalis	Western Gull	2	4
Larus marinus	Great Black-Backed Gull	4	8
Rhodostethia rosea	Ross's Gull	2	3
Sterna maxima	Royal Tern	2	4

Larosterna inca	Inca Tern	2	4
Sterna anaethetus	Bridled Tern	2	4
Rynchops niger	Black Tern	2	4
Gygis alba	White Tern	2	4
Anous tenuirostris	Lesser Noddy	1	2
Cursorius temminickii	Temnick's Courser	1	2
Glareola pratincoa	Common Pratincole	1	2
Bartramia longicauda	Upland Sandpiper	2	4
Numenius phaeopus	Whimbrel	2	4
Charadrius vociferus	Killdeer	2	4
Charadrius wilsonia	Wilson's Plover	2	4
Sula dactylatra	Masked Booby	7	14
Morus capensis	Cape Gannet	5	10
Morus bassanus	Northern Gannet	6	12
Phalacrocorax malaneoleucus	Little Pied Cormorant	6	5
Phalacrocorax varius	Australian Pied Cormorant	1	2
Phalacrocorax atriceps	Imperial Shag	5	5
Phalacrocorax magellanicus	Magellanic Cormorant	6	12
Palacrocorax carbo	Great Cormorant	2	4
Phalacrocorax auritus	Double-Crested Cormorant	2	4
Anhinga melanogaster	Indian Darter	1	1
Anhinga anhinga	American Darter	1	1
Fregata ariel	Lesser Frigate Bird	2	4
Fregata magnificens	Magnificent Firgate Bird	2	4
Ardea alba	Great Egret	2	4
Ardea herodius	Great Blue Heron	2	4
Cochlaerius cochlaerius	Boat-Billed Heron	2	4
Eudocimus ruber	Scarlet Ibis	2	2
Pelecanus occidentalis	Brown Pelican	4	8
Pelecanus onocrotalis	Great White Pelican	2	3
Pelecanus erythororhychos	American White Pelican	2	4
Pterodroma externa	Juan Fernandez Petrel	2	4
Pterodroma neglecta	Kermadec Petrel	2	4
Pterodroma inexpectata	Mottled Petrel	2	2
Fulmaris glacials	Northern Fulmar	2	4
Fulamris carneipes	Flesh-Footed Shearwater	2	4
Puffinus gravis	Great Shearwater	3	6
Puffinus griseus	Sooty Shearwater	4	8
Pelecanoides garnotii	Peruvian Diving Petrel	6	18
Pelecanoides urinatrix	Common Diving Petrel	5	9
Thalassarche cauta	White Capped Albatross	2	4
Thalassarche melanophris	Black-browed Albatross	2	4
Phoebastria immutabilis	Laysan Albatross	2	4
Diomedia exulans	Shy Albatross	4	8

Oceanodroma furcata	Fork-Tailed Storm Petrel	2	4
Oceanities oceanities	Wilson's Storm Petrel	2	3
Aptenodytes fosteri	Emperor Penguin	7	12
Aptenodytes patagonicus	King Penguin	3	4
Spheniscus humboldti	Humbolt Penguin	5	8
Spheniscus megallanicus	Magellanic Penguin	2	4
Spheniscus demersus	African Penguin	2	4
Eudyptula minor	Little Blue Penguin	2	4
Eudyptes pachyrhynchus	Fiorland Penguin	1	2
Eudyptes crysocome	Rock Hopper Penguin	2	4
Eudyptes chrysolophus	Macaroni Penguin	1	2
Pygoscelis adeliae	Adelie Penguin	4	7
Gavia immer	Common Loon	10	18
Gavia stellata	Red-Throated Loon	2	4
Gavia pacifica	Pacific Loon	2	4
Aechomorphus occidentalis	Western Grebe	2	4
Corythaixoides concolor	Grey Go-Away Bird	1	1
Musophaga rossae	Ross's Turaco	1	1

References

Adams N J, Walter C B (1993) Maximum diving depths of Cape Gannets. *The Condor*. 95, 734-736.

Austin J J, Bretagnolle V, Pasquet E (2004) A global molecular phylgeny of the small Puffinus shearwaters and implications for systematics of the little-audubon's shearwater complex. *The Auk*. 121, 847-864.

Baker A J, Pereira S L, Paton T A (2007) Phylogenetic relationships and divergence times of Charadriiformes genera: multigene evidence for the Cretaceous origin of at least 14 clades of shorebirds. *Biology Letters. 3,* 205-210.

Beletsky, L., & Nurney, D. (2006). *Birds of the world*. Baltimore,MD: Johns Hopkins University Press.

Bethge P, Nicol S, Culik B M, et al. (1997) Diving behaviour and energetics in breeding little penguins (Eudyptula minor). *Journal of Zoology*. 242, 483-502.

Brown R G B, Barker S P, Gaskin D E, et al. (1981). The foods of Great and Sooty Shearwaters *Puffinus gravis* and *P. griseus* in eastern Canadian waters. *Ibis*. 123, 19-30.

Burger A E, Powell D W (1990). Diving depths and diet of Cassin's auklet at Reef Island, British Columbia. *Canadian Journal of Zoology*. ***68***(7), 1572-1577.

Burger A E, Simpson M (1986) Dive Depths of Atlantic Puffins and Common Murres. *The Auk*. 103, 828-830.

Burger A E, Wilson R P, Garnier D, et al. (1993) Diving depths, diet, and underwater foraging of Rhinoceros Auklets in British Columbia. *Canadian Journal of Zoology*. 71, 2528-2540.

Burger A E (2001) Diving depths of Shearwaters. *The Auk*. 118, 755-759.

Cairns D K (1988). Seabirds as indicators of marine food supplies. *Biological Oceanography*. 5(4), 261-271.

Coulombre A J, Coulombre J L, Mehta H (1962) The skeleton of the eye. II. Overlap of the scleral ossicles of the domestic fowl. *Developmental Biology*. 5, 382–401.

Cook T R, Lescroel A, Yann T et al. (2008) To Breathe or not to breathe? Optimal breathing, aerobic dive limit and oxygen stores in deep-diving blue-eyed shags. *Animal Behavior*. 76, 565-576.

Cracraft J (1985) Monophyly and phylogenetic relationships of the pelecaniformes: a numerical cladisitic analysis. *The Auk*. 102, 834-853

Creuzet S, Vincent C, Couly G (2005) Neural crest derivatives in ocular and periocular structures. *Internal Journal of Developmental Biology*. *49*, 161-171.

Croll D A, Gaston A J, Burger A E, et al. (1992). Foraging behavior and physiological adaptation for diving in thick-billed murres. *Ecology*. 344-356.

Cronin T W (2012) Visual Optics: Accommodation in a Splash. *Current Biology* 22, 871-873.

Croxall J P, Lishman G S (1987) The food and feeding ecology of penguins. *Seabirds: feeding ecology and role in marine ecosystems*. Cambridge University Press, Cambridge, 101-133.

Croxall J P, Briggs D R, Kato A, et al. (1993) Diving pattern and performance in the macaroni penguin Eudyptes chrysolophus. Journal of Zoology. 230, 31-47.

Curtis E L, Miller, R C (1938) The Sclerotic Ring in North American Birds. The Auk. 55, 225 - 243.

Day R H, Prichard A K, Nigro D A (2003) Ecological Specialization and Overlap of Brachyramphus Murrlets in Prince William Sound, Alaska. The Auk. 120, 680-699.

de Queiroz K (1982) The scleral ossicles of sceloporine iguanids: a reexamination with comments on their phylogenetic significance. Herpetologica. 38, 302-311.

de Queiroz K, Good D A (1988) The scleral ossicles of Opisthocomus and their phylogenetic significance. The Auk. 105, 29-35.

Hall B K (1981) Specificity in the differentiation and morphogenesis of neural-crest-derived sclera ossicles and of epithelial sclera papillaw in the eye of the embryonic chick. *Journal of Embryology & Experimental Morphology*. 66, 175-190.

del Hoyo J D, Elliott A, Sargatal J, & Cabot J (1996). Handbook of the Birds of the World. *Lynx Edicions, Barcelona*.

Ewins P J (1993) Pigeon Guillemot (*Cepphus columba*). *The Birds of North America,* Philadelphia: The Academy of Natural Sciences.

Forey P L, Young, V T (1985). Acanthodian and coelacanth fish from the Dinantian of Foulden, Berwickshire, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*. 76, 53-59.

Franz-Odendaal T A (2005) Intramembranous ossification of scleral ossicles in *Chelydra serpentina.* Zoology. 109, 75-81.

Franz-Odendaal T A (2008) Toward understanding the development of scleral ossicles in the chicken, Gallus gallus. *Developmental Dynamics*. 237, 3240 – 3251.

Franz-Odendaal TA (2008) Scleral ossicles of Teleostei: Evolutionary and Developmental Trends. *The Anatomical Record*. 291, 161-168.

Franz-Odendaal T A, Hall B K (2006) Skeletal elements within teleost eyes and a discussion of their homology. *Journal of Morphology*. 267, 1326-1337.

Franz-Odendaal T A, Vickaryous M A (2006) Skeletal elements in the vertebrate eye and adnexa: morphological and developmental perspectives. *Developmental Dynamics*. 235, 1244 – 1255.

Gaston A J, Jones I L, Lewington I (1998) *The auks*. Oxford: Oxford University Press.

Glasser A, Howland H C (1996) A History of Studies of Visual Accommodation in Birds. *The Quarterly Review of Biology*. 71, 475-509.

Grémillet D, Wilson R P, Storch S (1999) Three-dimensional space utilization by a marine predator. *Marine Ecology Progress Series*. 183, 263 – 273.

Gugg W (1939) Der Skleralring der plagiotremen Reptilien. *Zoologische Jahrbücher. Abteilung für Anatomie*. 65, 339-416.

Hackett S J, Kimball R T, Reddy S, et al. (2008) A phylogenomic study of birds reveals their evolutionary history. *Science*. 320, 1763.

Hall B K (1981) Specificity in the differentiation and morphogenesis of neural-crest-derived sclera ossicles and of epithelial sclera papillae in the eye of the embryonic chick. *Journal of Embryology & Experimental Morphology*. 66, 175-190.

Hall M I (2008) The anatomical relationships between the avian eye, orbit and sclerotic ring: implications for inferring activity patterns in extinct birds. *Journal of Anatomy*. 212, 781-794.

Hall M I, Ross C F (2007) Eye shape and activity pattern in birds. *Journal of Zoology*. 271, 437-444.

Hedd A, Gales R, Brothers N, et al. (1997) Diving Behaviour of the Shy Albatross Diomedia cauta in Tasmania: Initial findings and dive recorded assessment. *Ibis*. 139, 8.

Howland C H, Sivak J G (1984) Penguin Vision in Air and Water. *Vision Research*. 24, 1905-1909.

Hull, C L (2000) Comparative diving behaviour and segregation of the marine habitat by breeding Royal Penguins, Eudyptes schlegeli, and eastern Rockhopper Penguins, Eudyptes chrysocome filholi, at Macquarie Island. *Canadian Journal of Zoology*. 78, 333-345.

Jahncke J, Zavalaga C B (1997) Maximum dive depths of the Peruvian diving-petrel. *Condor*. 99, 1002 - 1004.

Jerlov (1969) *Optical Oceanography*. Amsterdam: Elsevier Publishing Company

Jones I (1993) Crested auklet. *The Birds of North America*, 1-15.

Kato A, Croxall J P, Watanuki Y et al. (1992) Diving patterns and performance in male and female Blue-eyed Cormorants *Phalacrocorax atriceps* at South Georgia. *Marine Ornithology*. 19, 117–129.

Kennedy M, Gray R D, Spencer H G (2000) The phylogenetic relationships of the shags and cormorants: can sequence data resolve a disagreement between behavior and morphology?. *Molecular Phylogenetics and Evolution*. 17, 345-359.

Kennedy M, Page R D (2002) Seabird supertrees: combining partial estimates of procellariiform phylogeny. *The Auk*. 119, 88-108.

Kooyman G L, Cherel Y, Le Maho Y, et al. (1992). Diving behavior and energetics during foraging cycles in king penguins. *Ecological Monographs*. 143-163.

Kooyman G L, Drabek C M, Elsner R, et al. (1971). Diving Behavior of the Emperor Penguin, *Aptenodytes forsteri*. *The Auk* 88(4), 775-795.

Kooyman G L (1975) Behavior and physiology of diving. *Biology of Penguins*. London: Macmillan Press Limited.

Kooyman G L, Cherel Y, Le Maho Y, et al. (1992). Diving behavior and energetics during foraging cycles in king penguins. *Ecological Monographs*, 143-163.

Kramer, M A (1991) Nonlinear principal component analysis using auto associative neural networks. *American Institute of Chemical Engineers Journal* 37, 233-243.

Ksepka D T, Bertelli S, Giannini, N P (2006) The phylogeny of the living and fossil Sphenisciformes (penguins) *Cladistics*. 22, 412-441.

Ksepka D T, Clarke, J A (2010) The basal penguin (Aves: Sphenisciformes) *Perudyptes devriesi* and a phylogenetic evaluation of the penguin fossil record. *Bulletin of the American Museum of Natural History*. 337, 1-77.

Kuroki M, Kato A, Watanuki Y, Niizuma Y, et al. (2003). Diving behavior of an epipelagically feeding alcid, the Rhinoceros Auklet (*Cerorhinca monocerata*). *Canadian Journal of Zoology* 81(7), 1249-1256.

Land M F (1981) Optics and vision in invertebrates. In M F Land, S B Laughlin, D R Nässel, N J Strausfeld, & T H Waterman (Eds.), *Comparative physiology and evolution of vision in invertebrates. B: Invertebrate visual centers and behavior I*, 471–592. Berlin, Heidelberg, New York: Springer–Verlag.

Lemmrich W (1939) DerSkleralring der Vogel. *Jenaische Zeitschrift fur Medizin und Naturwissenschaft*. 65, 513-586.

Luna-Jorquera G, Culik B M (1999) Diving behavior of Humbldt Penguins *Spheniscus humboldti* in Northern Chile. *Marine Ornithology*. 27, 67-76.

Lima F C, Vieira L G, Santos A L Q et al. (2009). Anatomy of the scleral ossicles in brazilian birds. *Brazilian Journal of Morphological Science*. 26, 165-9.

Lythgoe J N (1979) *The Ecology of Vision*. Oxford: Clarendon Press.

Maddison W P, Maddison D R (2011) Mesquite: a modular system for evolutionary analysis. Version 2.75, http://mesquiteproject.org

McCracken K G, Sheldon F H (1998) Molecular and osteological heron phylogenies: sources of incongruence. *The Auk*. 115, 127-141.

Martin G R (1985) Eye. In King A S, McLelland J (Eds.), *Form and function in birds III*. 311-373. London: Academic Press.

Martin G R (1998) Eye Structure and amphibious foraging in albatrosses. *The Royal Society*. *B* 265, 665-671.

Martin G R (1999) Eye structure and foraging in King Penguins Aptenodytes patagonicus. *Ibis* 141, 444-450

Martin G R, Young S R (1984) The eye of the Humboldt Penguin, *Spheniscus humboldti*: visual fields and schematic optics. *Royal Society of London*. 223, 197-223.

MATLAB 8.0 and Statistics Toolbox 8.1, The MathWorks, Inc., Natick, Massachusetts, United States.

Nesbitt S J, Turner A H, Weinbaum J C (2012). A survey of skeletal elements in the orbit of Pseudosuchia and the origin of the crocodylian palpebral. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*. 103, 365-381.

Nunn G B, Stanley S E (1998) Body size effects and rates of cytochrome b evolution in tube-nosed seabirds. *Molecular Biology and Evolution*. 15, 1360-1371.

Pagel (1999) Infering patterns of biological evolution. *Nature*. 401, 877-84.

Piatt, J F, Nettleship, D N (1985) Diving Depth of Four Alcids. *The Auk*. 102, 293-297.

Piatt, J F, Nettleship D N (1985) *The Atlantic Alcidae*: *The Evolution, Distribution, and Biology of the Auks Inhabiting the Atlantic Ocean and Adjacent Water Areas*. London: Academic Press.

Prince P A, Huin N, Weimerskirch, H (1994) Diving depths of albatrosses. *Antarctic Science*. 6, 353-354.

Prince P A, Jones M (1992) Maximum dive depth attained by south Georgian diving petrel *Pelecanoides georgicus* at bird island, south Georgia. *Antarctic Science*. 4, 433-434.

Quiantana F, Wilson R P, Yorio, P (2007) Dive Depth and plumage air in wettable birds: the extraordinary case of the imperial cormorant. *Marine Ecology Press Series* 334, 299-310.

Roby D D, Ricklefs R E (1986) Energy expenditure in adult least auklets and diving petrels during the chick-rearing period. *Physiological zoology*, 661-678.

Sanger, T D (1989). Optimal unsupervised learning in a single-layer linear feedforward neural network. *Neural networks*, 2(6), 459-473.

Schmitz L (2009) Quantitative estimates of visual performance features in fossil birds. *Journal of Morphology* 270, 759-773.

Schmitz L, Motani R (2010) Morphological differences between the eyeballs of nocturnal and diurnal amniotes revisited from optical perspectives of visual environments. *Vision Research*. 50, 936-946.

Scolaro J A, Suburo A M (1991) Maximum Diving Depths of the Magellanic Penguin (Profundidad de Buceo del Pingüino de Magallanes). *Journal of Field Ornithology*, 204-210.

Sivak, J G, Lincer J L, Bobier W (1977) Amphibious visual optics of the eyes of the double-crested cormorant (*Phalacrocorax auritus*) and the brown pelican (Pelecanus occidentalis). *Canadian Journal of Zool*ogy 55, 782-788.

Sivak J G, Millodot M (1977) Opitcal Performance of the Penguin Eye in Air and Water. *Journal of Comparative Physiology*. 119*, 241-247*.

Sivak J G, Vrablic O E (1978) The anatomy of the eye of the Adelie penguin with special reference to optical structure and intraocular musculature. *Canadian Journal of Zoology*. 57, 346-352.

Sivak J G (1980) Avian mechanisms for vision in air and water. *Trends in Neuroscience*. 3, 314-317.

Sivak J G, Hildebrand T, Lebert C (1985) Magnitude and rate of accommodation in diving and non-diving birds. *Vision Research*. 25, 925-933.

Sivak J G, Hildebrand T E, Lebert, C G, et al. (1986) Occular accommodation in chickens: Corneal versus lenticular accommodation and effect of age. *Vision Research*. 25, 1865-1872

Smith N A (2011) Taxonomic revision and phylogenetic analysis of the flightless mancallinae (Aves Pan-Alcidae). *Zoological Keys*. 91, 1-116.

Suburo,A M (1988) The Structure of the Eye in *Spheniscus magellanicus*: Dimensions of the Cornea and Lens in Different Age Groups. *Colonial Aquatic birds*. 11, 227-233.

Suburo A M (1990) The Eye of the Magellanic Penguin (*Spheniscus magellanicus*): Structure of the Anterior Segment *The American Journal of Anatomy* 189, 245-252.

Taylor G A (2008) Maximum dive depths of eight New Zealand Procellariiformes, including Pterodroma species. *Papers and Proceedings of the Royal Society of Tasmania*. 142, 89-97.

Thewissen J G, Nummela S (2008) On Becoming Aquatic. *Sensory Evolution on the Threshold: Adaptations in Secondarily Aquatic Vertebrates*. Los Angeles: University of California Press.

Underwood G (1970) The eye. *Biology of the Reptilia Vol 2*. London: Academic Press.

Von Den Driesch A (1976) *A guide to the measurement of animal bones from archaeological sites: as developed by the Institut für Palaeoanatomie, Domestikationsforschung und Geschichte der Tiermedizin of the University of Munich*. Peabody Museum Press.

Walls G L (1942) *The Vertebrate Eye and Its Adaptive Radiation*. Bloomfield Hills, MI: Cranbook Institute of Science.

Wanless S, Bacon P J, Harris M P, et al. (1997) Modelling environmental and energetic effects on feeding performance and distribution of shags (Phalacrocorax aristotelis): integrating telemetry, geographical information systems, and modeling techniques *ICES Journal of Marine Science: Journal du Conseil*. 54, 524-544.

Wang X, Clarke J A (2014) Phylogeny and forelimb disparity in waterbirds. *Evolution*. 68, 2847-2860.

Watanuki Y, Kato A, Naito Y (1996) Diving performance of male and female Japanese cormorants. *Canadian Journal of Zoology*. 74, 1098-1109.

Watanuki Y, Burger A E (1999) Body mass and dive duration in alcids and penguins. *Canadian Journal of Zoology*. 77, 1838-1842.

Watanuki Y, Wanless S, Harris M, et al. (2006) Swim speeds and stroke patterns in wing-propelled divers: a comparison among alcids and a penguin. *Journal of Experimental Biology* 209, 1217-1230.

Warheit K I, Good D A, de Queiroz, K (1989) Variation in numbers of scleral ossicles and their phylogenetic transformations within the Pelecaniformes. *The Auk*. 106, 383-388.

Zavalaga C B, Jahncke J (1997) Dive depths of the Peruvian diving-petrel. *The Condor*. 99, 1002-1004.